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An Appraisal of the Higher Classification of Cicadas (Hemiptera: Cicadoidea) with Special Reference to the Australian Fauna

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ABSTRACT. The history of cicada family classification is reviewed and the current status of all previously proposed families and subfamilies summarized. All tribal rankings associated with the Australian fauna are similarly documented. A cladistic analysis of generic relationships has been used to test the validity of currently held views on family and subfamily groupings. The analysis has been based upon an exhaustive study of nymphal and adult morphology, including both external and internal adult structures, and the first comparative study of male and female internal reproductive systems is included. Only two families are justified, the Tettigarctidae and Cicadidae. The latter are here considered to comprise three subfamilies, the Cicadinae, Cicadettinae **n.stat.** (= Tibicininae *auct.*) and the Tettigadinae (encompassing the Tibicinini, Platypediidae and Tettigadidae). Of particular note is the transfer of *Tibicina* Amyot, the type genus of the subfamily Tibicininae, to the subfamily Tettigadinae. The subfamily Plautillinae (containing only the genus *Plautilla*) is now placed at tribal rank within the Cicadinae. The subtribe Ydiellaria is raised to tribal rank. The American genus *Magicicada* Davis, previously of the tribe Tibicinini, now falls within the Taphurini. Three new tribes are recognized within the Australian fauna, the Tamasini **n.tribe** to accommodate *Tamasa* Distant and *Parnkalla* Distant, Jassopsaltriini **n.tribe** to accommodate *Jassopsaltria* Ashton and Burbungini **n.tribe** to accommodate *Burbunga* Distant. Additional tribal changes occur within the Australian fauna: *Anapsaltoda* Ashton, *Arenopsaltria* Ashton, *Henicopsaltria* Stål, *Neopsaltoda* Distant and *Psaltoda* Stål are transferred from Cyclochilini to Cryptotympanini leaving Cyclochilini monotypic; *Chrysocicada* Boulard is transferred from Parnisini to Taphurini; *Diemeniana* Distant, *Gudanga* Distant and *Quintilia infans* (Walker) (representing a new genus) from Parnisini to Cicadettini; and *Marteena* Moulds and *Abricta borealis* (Goding & Froggatt) (the latter also representing a new genus) from Taphurini to Cicadettini. A new subtribe is proposed in the tribe Taphurini, Tryellina **n.subtribe**. Diagnostic descriptions are provided for all families, subfamilies, tribes and subtribes treated in this work. Keys to families and subfamilies are presented together with a key to the tribes of Australian Cicadoidea.

Terminologies for external and internal morphology of the Cicadoidea are summarized in 30 detailed figures. New structures and features of significant taxonomic importance are identified and named. A stridulatory mechanism found in the Australian genus *Cyclochila* is described for the first time.

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INTRODUCTION

The historical review below highlights differences of opinion between systematists in family and subfamily classification of the Cicadoidea (cicadas). Family and subfamily classifications have been traditionally based on structures associated with sound production and communication but the validity of these classifications has never been tested by modern cladistic methodologies. There is similar justification for a review of tribal groupings which, for the most part, remain those of Distant (1906b).

This paper aims at addressing the above problems, particularly as they relate to the Australian fauna. A phylogenetic analysis of all Australian genera has been extended to include key representatives of genera from all tribes associated with the Australian fauna, and of all families and subfamilies previously proposed within the Cicadoidea except Ydiellinae (reduced by Boulard, 1993, to subtribal rank). The complex question of the placement of the cicadas within the Hemiptera falls beyond the scope of this paper and is not considered.

The phylogenetic analysis employs cladistic methodologies based upon morphology of nymphs and adults. Results draw the following main conclusions. The Cicadoidea are best divided into two families, the Tettigarctidae and Cicadidae, and the Cicadidae are further best divided into three subfamilies, the Cicadinae, Cicadettinae **n.stat.** (= Tibicininae *auct.*) and Tettigadinae. Twelve tribal groupings best represent the Australian Cicadidae, including three new tribes and the abolition of two others from the Australian fauna. A new subtribe is proposed in the Taphurini.

The American periodical cicada genus *Magicicada* Davis is transferred from the Tibicinini to the Taphurini. Tribal changes within the Australian fauna include the transfer of *Anapsaltoda* Ashton, *Arenopsaltria* Ashton, *Henicopsaltria* Stål, *Neopsaltoda* Distant and *Psaltoda* Stål from Cyclochilini to Cryptotympanini leaving Cyclochilini monotypic; *Chrysocicada* Boulard from the Parnisini to the Taphurini, *Diemeniana* Distant, *Gudanga* Distant and *Quintilia infans* (Walker) (representing a new genus) from Parnisini to Cicadettini; and *Marteena* Moulds and *Abricta borealis* (Goding & Froggatt) (the latter also representing a new genus) from Taphurini to Cicadettini.

Diagnostic descriptions are provided for all families and subfamilies; similarly for all tribes and subtribes associated with the Australian fauna. Keys to families, subfamilies and tribes are presented. A previously unrecognized stridulatory mechanism found on species of the Australian genus *Cyclochila* is also documented.

This study was made primarily to place Australian genera in a family hierarchy and many non-Australian genera were omitted for practical reasons, especially from Africa, South America and southeast Asia.

This work is divided into four main sections: "Terminology" which provides an overview of morphological structures and their names, "Historical reviews" part of which includes an overview of family group names, "Phylogenetic analysis" which reviews the family classification of the Cicadoidea, and "Taxonomy" which formally redefines family, subfamily and tribal groupings.

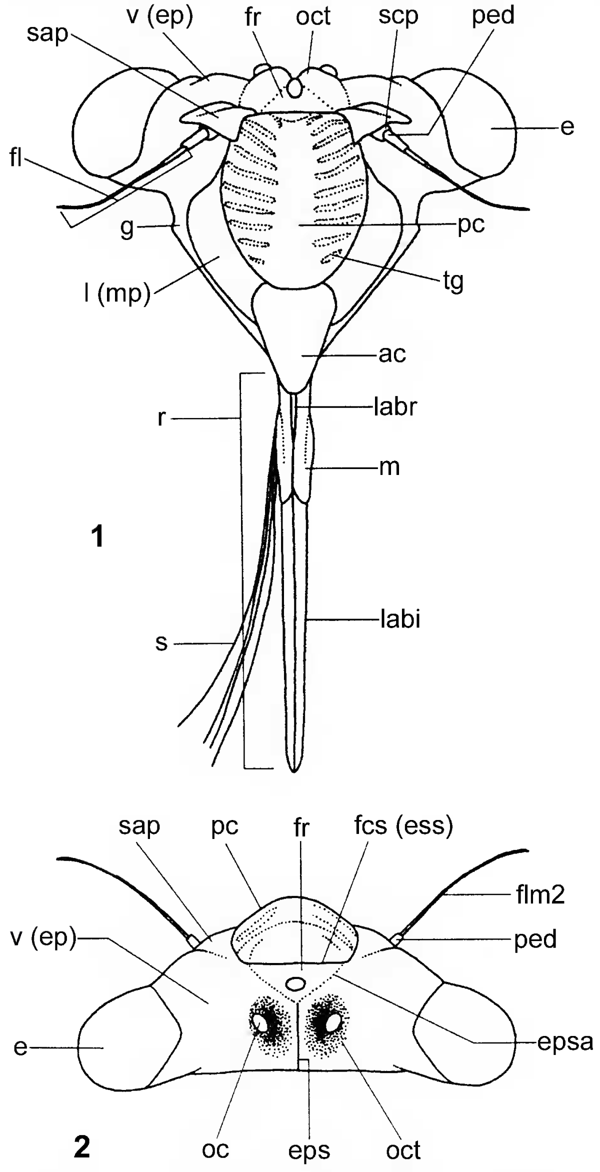
TERMINOLOGY

In-depth studies of cicada morphology include those of Kramer (1950), Matsuda (1965, 1970, 1976), Boulard (1965), Hamilton (1981), Dworakowska (1988) and Sweet (1996). Authors providing comprehensive summaries of cicada morphology and associated terminologies include J.G. Myers (1928), Pesson (1951), Kato (1956), Duffels (1977) and Boulard (1996a).

While there are few differences of opinion concerning structural interpretation between these authors, there are considerable differences in the terminologies used, and in the depth of treatment of major features. No single work provides terminologies for all structures referred to in this paper. Summaries of some alternative terminologies are provided by Dashman (1953), Hamilton (1981) and Blocker & Triplehorn (1985). Terminologies adopted here are those I consider to represent best the broad consensus of cicada systematists. In an attempt to provide a broad base line of morphological terms, some terminology included below is not referred to in this work.

Head (Figs. 1, 2). Terminology mostly follows that of Kramer (1950). Interpretations of sutures follows a more extensive study of head morphology by Hamilton (1981). Hamilton also provides a useful list of synonyms for head structures.

Thorax (Figs. 3, 4). Terminology for the dorsum of the thorax (Fig. 3) follows "traditional" terminology used by cicada systematists (cf. Duffels, 1977). I introduce the following new term. The *scutal depressions* (sd) are structures previously ignored; they always lie a little mediad of the distal ends of the anterior arms of the cruciform elevation and may be associated with internal muscle attachment. The *submedian sigilla* (ssig) and *lateral sigilla* (lsig) are terminology introduced by Moulds (2002) for features previously carrying terminology loosely describing these as markings of various shapes; the submedian sigilla are always defined along their outer margins by the parapsidal sutures. They are a consequence of internal muscle attachments and are often darkly pigmented.



Figs. 1–2. Head, *Tamasa tristigma*, Cicadinae: (Fig. 1) anterior view; (Fig. 2) dorsal view. Terminology after Kramer (1950) and Hamilton (1981). Terminologies in brackets also in current use. (*ac*) anteclypeus; (*e*) compound eye; (*eps*) epicranial suture; (*epsa*) anterior arm of epicranial suture; (*fcs, ess*) frontoclypeal suture, or epistomal suture; (*fl*) flagellum of antenna; (*flm 2*) second flagellomere; (*fr*) frons; (*g*) gena; (*l, mp*) lorum, or mandibular plate; (*labi*) labium; (*labr*) labrum; (*m*) mentum; (*oc*) ocellus, median or lateral; (*oct*) ocular tubercle; (*pc*) postclypeus; (*ped*) pedicel; (*r*) rostrum; (*s*) stylets; (*sap*) supra-antennal plate; (*scp*) scape; (*tg*) transverse groove; (*v, ep*) vertex, or epicranium.

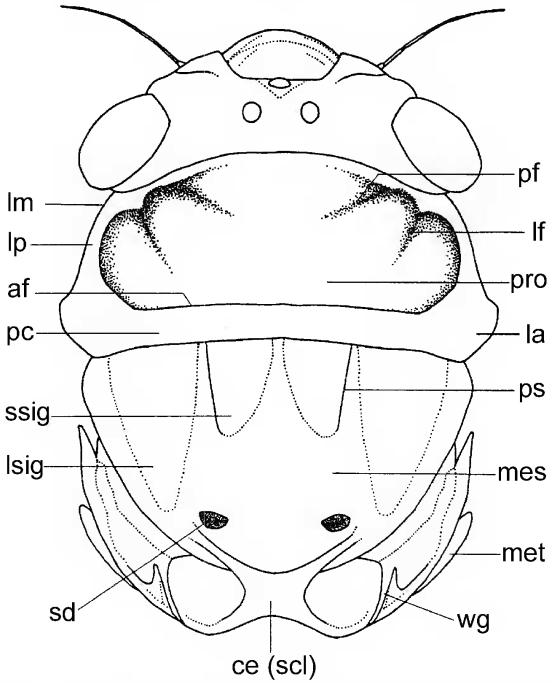


Fig. 3. Male thorax, dorsal view with head *in situ, Tamasa tristigma*, Cicadinae. Terminology modified from Duffels (1977). Terminologies in brackets also in current use. (*af*) ambient fissure of pronotum; (*ce, scl*) cruciform elevation, or scutellum; (*la*) lateral angle of pronotal collar; (*lf*) lateral fissure; (*lm*) lateral margin of pronotal collar; (*lp*) lateral part of pronotal collar; (*lsig*) lateral sigilla; (*mes*) mesonotum; (*met*) metanotum; (*pc*) pronotal collar; (*pf*) paramedian fissure; (*pro*) pronotum; (*ps*) parapsidal suture; (*sd*) scutal depression; (*ssig*) submedian sigilla; (*wg*) wing groove.

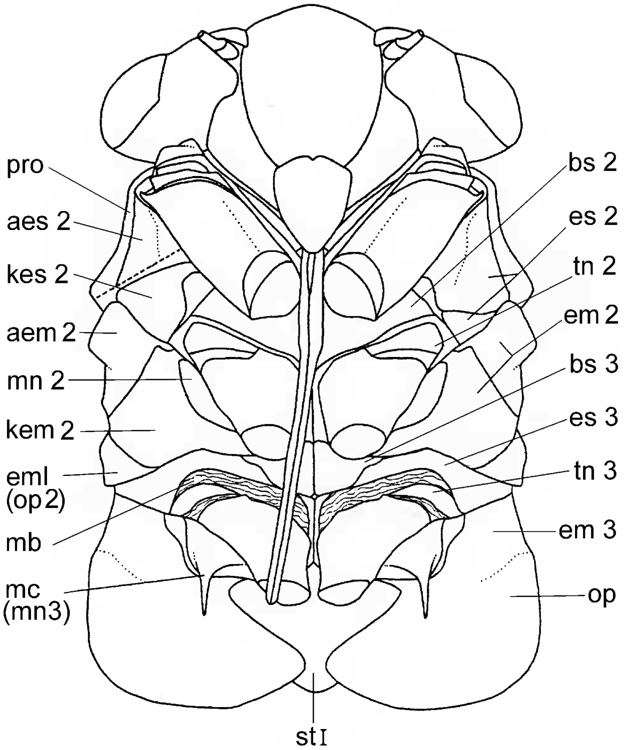


Fig. 4. Male thorax, ventral view with head *in situ* but legs detached except for coxae, *Tamasa tristigma*, Cicadinae. Terminology after Kramer (1950). Terminologies in brackets also in current use. (*aem 2*) anepimeron 2; (*aes 2*) anepisternum 2; (*bs 2*) basisternum 2; (*bs 3*) basisternum 3; (*eml, op 2*) epimeral lobe, or operculum 2; (*em 2*) epimeron 2; (*em 3*) remnant of epimeron 3; (*es 2*) episternum 2; (*es 3*) episternum 3; (*kem 2*) katepimeron 2; (*kes 2*) katepisternum 2; (*lm*) lateral margin of pronotal collar; (*mb*) membrane; (*mc, mn 3*) meracanthus, or meron 3; (*mn 2*) meron 2; (*op*) operculum (includes epimeron 3); (*pro*) underside of pronotum; (*st I*) abdominal sternite I; (*tn 2*) trochantin 2; (*tn 3*) trochantin 3.

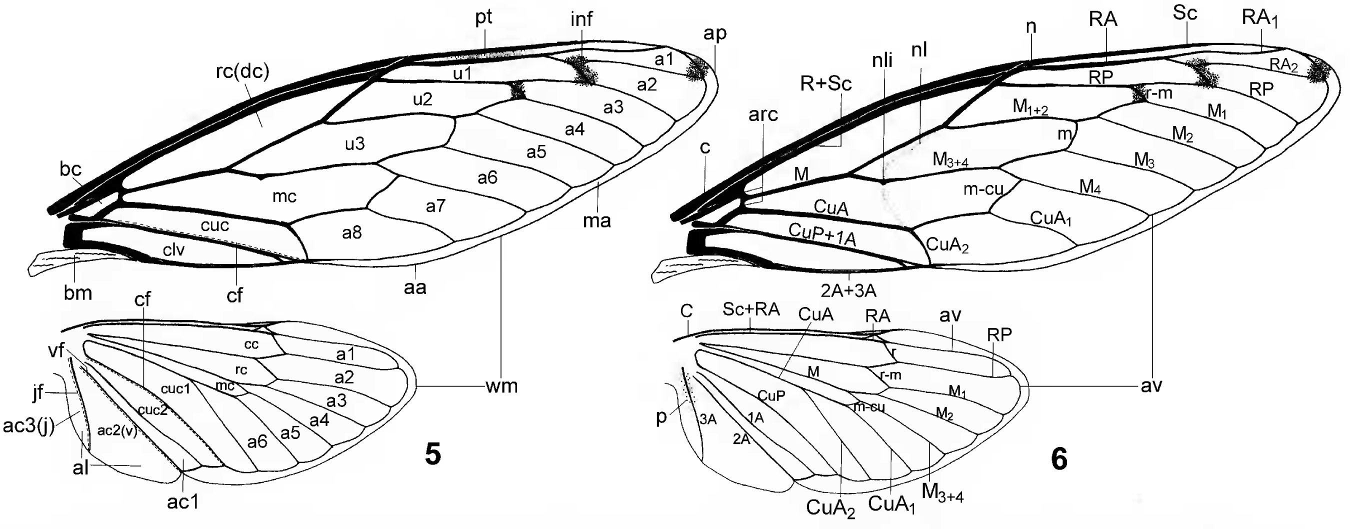
The apparent underside of the thorax (Fig. 4) is a complex of mostly sclerites of pleural origin, the sternal sclerites having been reduced and now barely visible along the ventral midline. There is some disagreement in interpretation of these sclerites among morphologists. I have adopted the interpretation of Kramer (1950) which, for the most part, incorporates a majority consensus and one with which I feel comfortable.

Wings (Figs. 5, 6). Vein notation originates from Kukalová-Peck (1983). The interpretation of veins follows that of Dworakowska (1988). The latter remains by far the most comprehensive study of wing venation available for the Auchenorrhyncha.

Legs (Figs. 7–11). Terminology follows classical terminologies for leg segments (cf. Imms, 1957; Lawrence *et al.*, 1991). Terminology relating to femoral spurs is my own as appropriate terminology is lacking in the literature.

Abdomen, excluding genitalia (Figs. 12, 13). Sweet (1996) provides an excellent account of cicada abdominal sclerites as part of an overview of the morphology of the pregenital abdomen of Hemiptera. Terminology is derived primarily from this work.

Male genitalia and reproductive system (Figs. 14–26). The male genitalia are contained by the capsule-like pygofer formed from the 9th abdominal segment. The uncus and claspers are derived from the 10th segment and the anal region from the 11th. The basally-hinged aedeagus housed within the pygofer is the copulatory outlet for the internal reproductive system; at rest it is secured by the uncus or the claspers (Fig. 25). There is a plethora of alternate terminologies for the various lobes and other features associated with these structures, many of which are summarized by Tuxen *et al.* (1970). For the most part I adopt a set of complementary terminology derived from

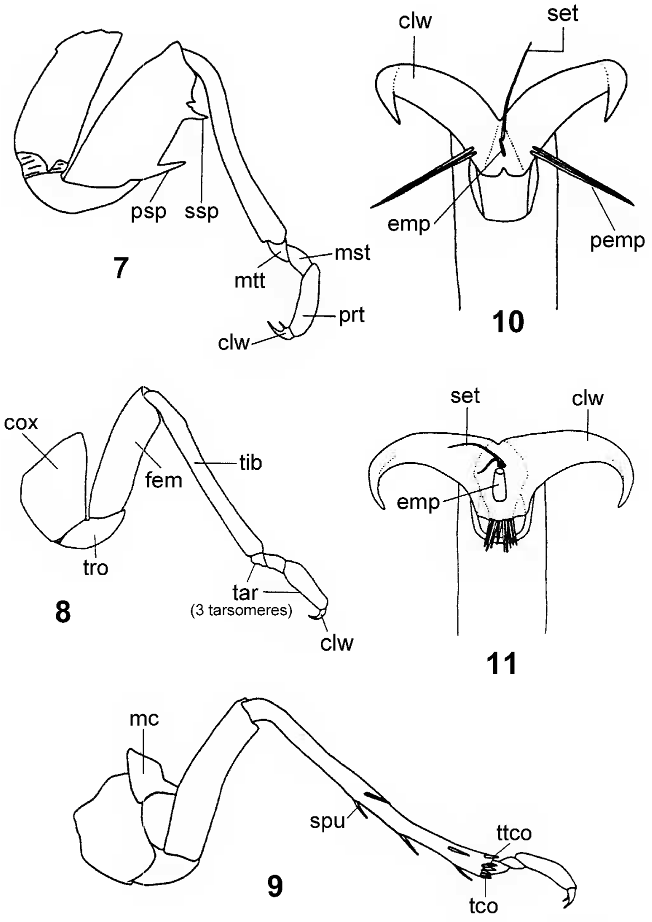


Figs. 5–6. Fore and hind wings, *Tamasa tristigma*, Cicadinae. Wing and cell notation (Fig. 5) adapted from Kukalová-Peck (1983) and Boulard (1996a) respectively; interpretation of venation (Fig. 6) after Dworakowska (1988). Terminologies in brackets are also in current use. (*A*) anal vein; (*a*) apical cell; (*aa*) anal angle; (*ac1*) anal cell 1; (*ac2(v)*) anal cell 2 or vannus; (*ac3, j*) anal cell 3 or jugum; (*al*) anal lobe (= ac2 + ac3); (*ap*) apex of wing; (*arc*) arculus; (*av*) ambient vein; (*bc*) basal cell; (*bm*) basal membrane; (*C*) costal vein; (*cc*) costal cell; (*cf*) claval fold; (*clv*) clavus; (*cuc*) cubital cell; (*CuA*) cubitus anterior vein; (*CuP*) cubitus posterior vein; (*inf*) infuscation; (*jf*) jugal fold; (*nli*) nodal line intersection; (*no*) node; (*M*) median vein; (*m*) medial crossvein; (*ma*) marginal area; (*mc*) medial cell, or ulnar cell 4 on fore wing; (*m-cu*) mediocubital crossvein; (*n*) node; (*nl*) nodal line; (*p*) plaga; (*pt*) pterostigma (pigmentation); (*R*) radius; (*r*) radial crossvein; (*RA*) radius anterior; (*rc, dc*) radial cell, or discal cell; (*r-m*) radiomedial crossvein; (*Sc*) subcostal vein; (*u*) ulnar cell; (*vf*) vannal fold; (*wm*) wing margin.

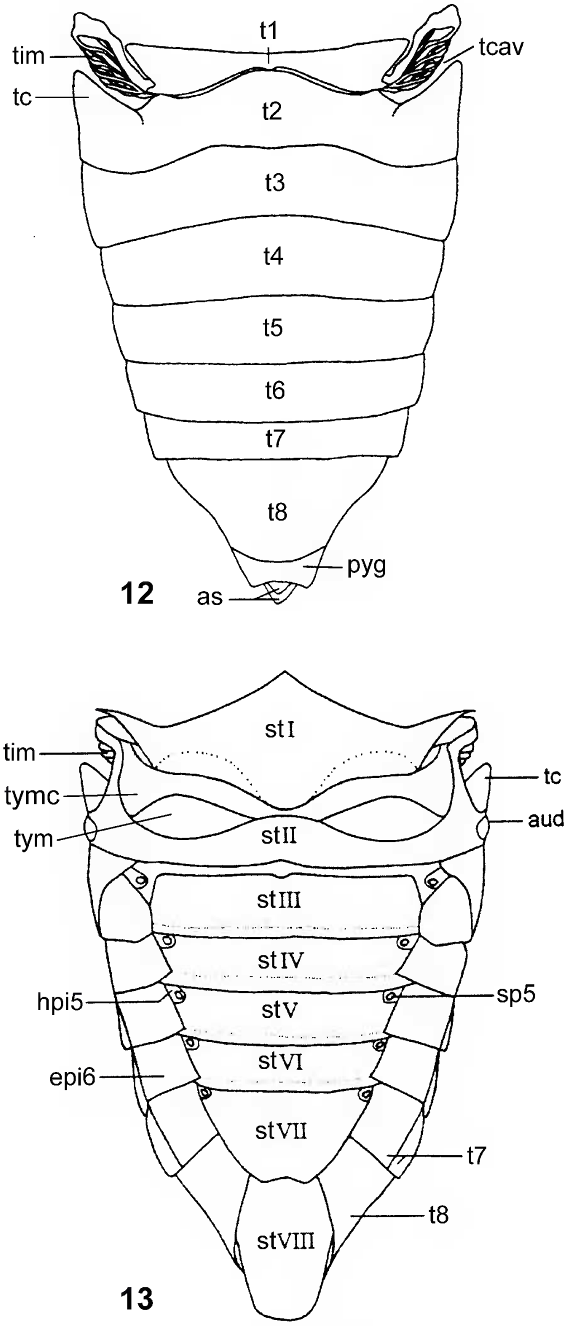
Duffels (1977), Dugdale (1972), Evans (1941) and Orian (1964). See also discussion of male genitalia under "Characters", p. 404.

Features of the internal reproductive system are shown in Fig. 26. In situ the testes are positioned forwards, always in the immediate vicinity of a pair of spiracles, usually those associated with sternite VI. The extensive tubulation is usually confined to the abdominal apex within segments 7 and 8. Terminology follows that of Matsuda (1976).

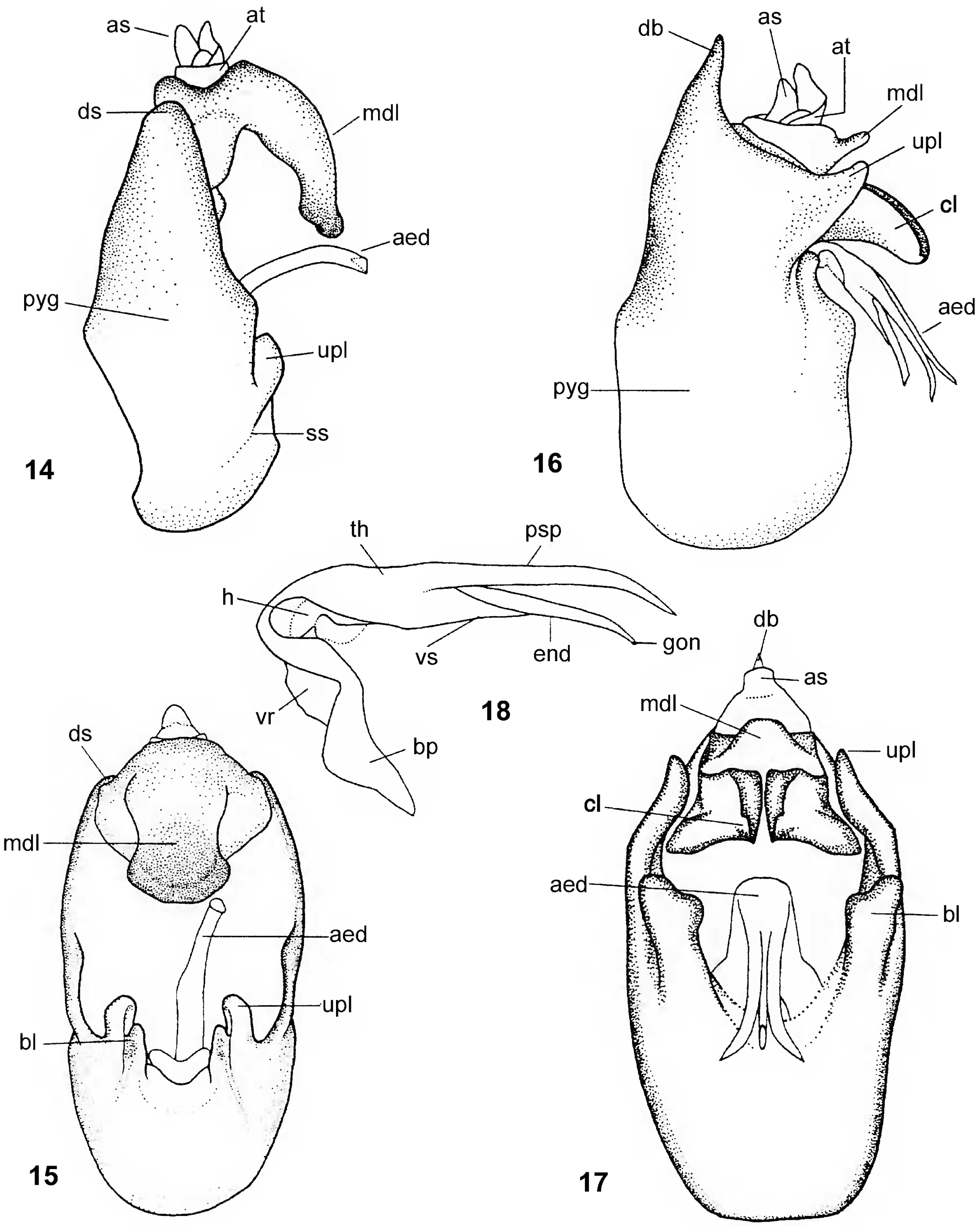
The inclusion of a secondary accessory gland on the vas deferens by Woodward *et al.* (1970) (figure repeated by Carver *et al.*, 1991) is considered erroneous. Their figure is identified as being a *Cicadetta* sp. but there are many such species so confirmation is impracticable. However, no such gland has come to my attention in other species of Cicadettini after many dissections and the likelihood of such an apomorphy arising within the tribe is highly improbable. The error most likely originated from a misinterpretation of the dissection from which the drawing was made; sometimes partially decomposing malpighian tubules adhere to genital tubules and a full dissection is usually required to reveal their alien nature.



Figs. 7–11. Legs, lateral view; pretarsal claws ventral view: (Fig. 7) fore leg, *Tamasa tristigma*, Cicadinae; (Fig. 8) mid leg, same species; (Fig. 9) hind leg, same species; (Fig. 10) pretarsus, same species; (Fig. 11) pretarsus *Tettigarcta crinita*, Tettigarctidae. Terminology mostly after Imms (1957). (*clw*) pretarsal claw (part of distal tarsomere); (*cox*) coxa; (*emp*) empodium; (*fem*) femur; (*mc*), meracanthus; (*mst*) mesotarsus; (*mtt*) metatarsus; (*pemp*) setiform parempodium; (*prt*) pretarsus; (*psp*) primary spine of fore femur; (*set*) sensory seta; (*spu*) tibial spur; (*ssp*) secondary spine of fore femur; (*tar*) tarsus; (*tib*) tibia; (*tco*) tibial comb; (*tro*) trochanter; (*ttco*) thumb of tibial comb.



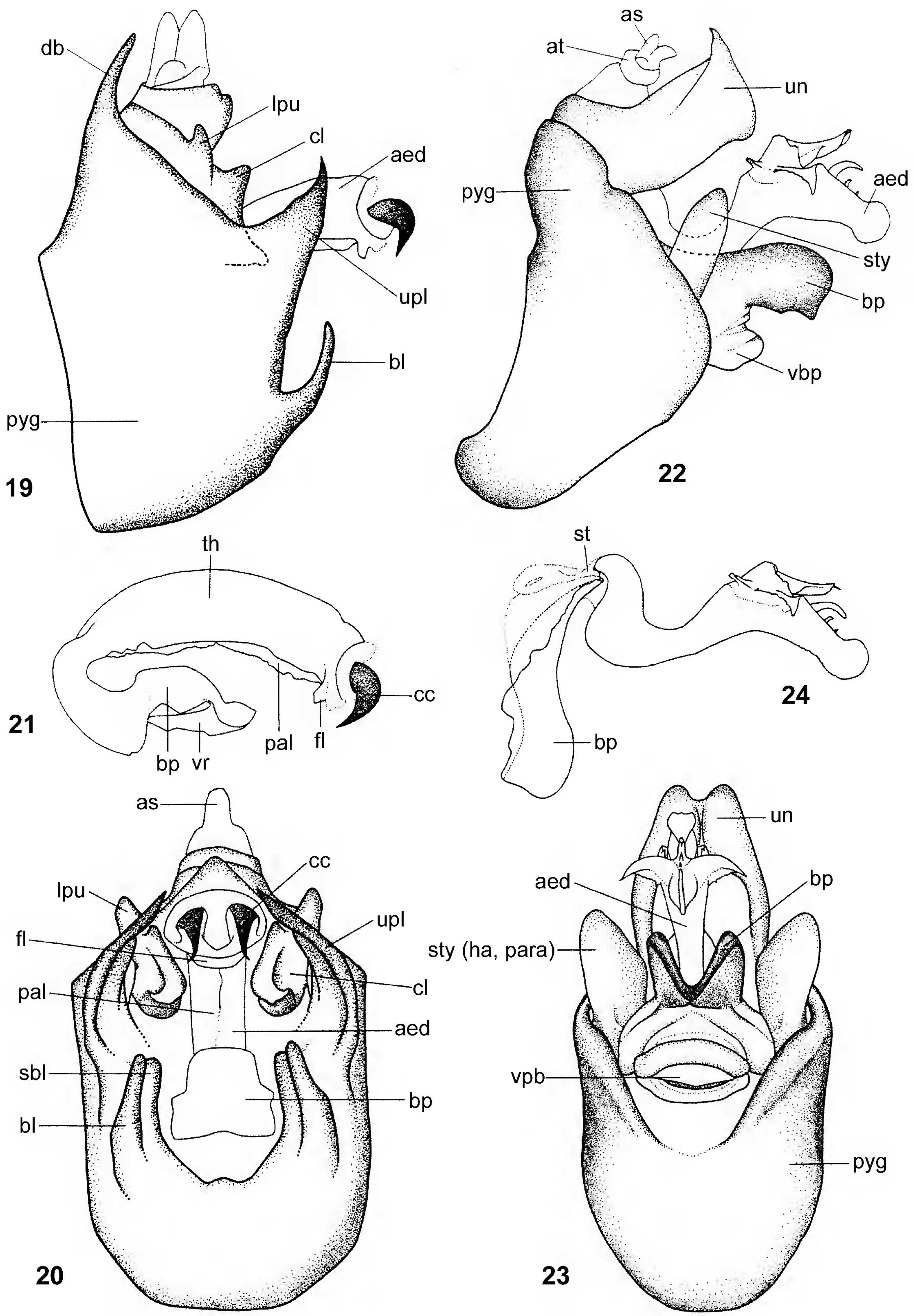
Figs. 12–13. Male abdomen, *Tamasa tristigma*, Cicadinae: (Fig. 12) dorsal view; (Fig. 13) ventral view. Terminology after Sweet (1996). (*as*) anal style; (*aud*) auditory capsule; (*epi*) epipleurite; (*hpi*) hypopleurite; (*pyg*) pygofer; (*sp*) spiracle; (*st*) sternite; (*t*) tergite; (*tc*) timbal cover; (*tcav*) timbal cavity; (*tim*) timbal; (*tym*) tympanum; (*tymc*) tympanal cavity.



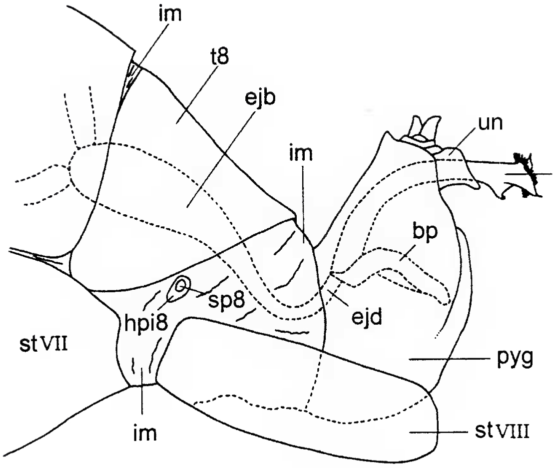
Figs. 14–18. Male genitalia: (Fig. 14) lateral view, *Neopsaltoda crassa*, Cicadinae; (Fig. 15) ventral view, same species; (Fig. 16) lateral view, *Kobonga umbrimargo*, Cicadettinae (= Tibicininae *auct.*); (Fig. 17) ventral view, same species; (Fig. 18) aedeagus, lateral view, same species. Terminology after Duffels (1977), Dugdale [1972] and Orian (1964). (*aed*) aedeagus; (*as*) anal styles; (*at*) anal tube; (*bl*) basal lobe of pygofer; (*bp*) basal plate; (*cl*) clasper; (*db*) dorsal beak; (*ds*) distal shoulder; (*end*) endotheca; (*gon*) gonopore; (*h*) hinge; (*mdl*) median lobe of uncus; (*psp*) pseudoparamere; (*pyg*) pygofer; (*ss*) sclerital suture; (*th*) theca; (*upl*) upper lobe of pygofer; (*vr*) ventral rib; (*vs*) ventral support.

Female genitalia and reproductive system (Figs. 27–30). The female external genitalia (Figs. 27, 28) are dominated by the 9th abdominal segment and the ovipositor. Terminology is based on that of Boulard (1996a).

The female internal reproductive system (Figs. 29, 30) is far more complex than that of the male. Many authors who have investigated the female reproductive system have failed to identify all elements involved; J.G. Myers (1928) gives an excellent historical account of the interpretation of the female reproductive system. Boulard (1965, 1996a) is the only author to have figured the entire female reproductive system. Terminology is largely derived from that of Boulard (1996a) with interpretations from Duffels (1977).



Figs. 19–24. Male genitalia: (Fig. 19) lateral view, *Tryella ochra*, Cicadettinae (= Tibicininae *auct.*); (Fig. 20) ventral view, same species; (Fig. 21) aedeagus, lateral view, same species; (Fig. 22) lateral view, *Tettigarcta crinita*, Tettigarctidae; (Fig. 23) ventral view, same species; (Fig. 24) aedeagus, lateral view, same species. Terminology after Duffels (1977), Dugdale (1972), Evans (1941), Moulds (2003) and Orian (1964). Symbols as for Figs. 14–18 plus: (*cc*) conjunctival claw; (*fl*) flabellum (*lpu*) lateral process of uncus; (*pal*) palearis; (*sbl*) secondary basal lobe of pygofer; (*st*) sinewation; (*sty*) (ha, para) style, harpago, or paramere; (*un*) uncus; (*vbp*) ventrobasal pocket.



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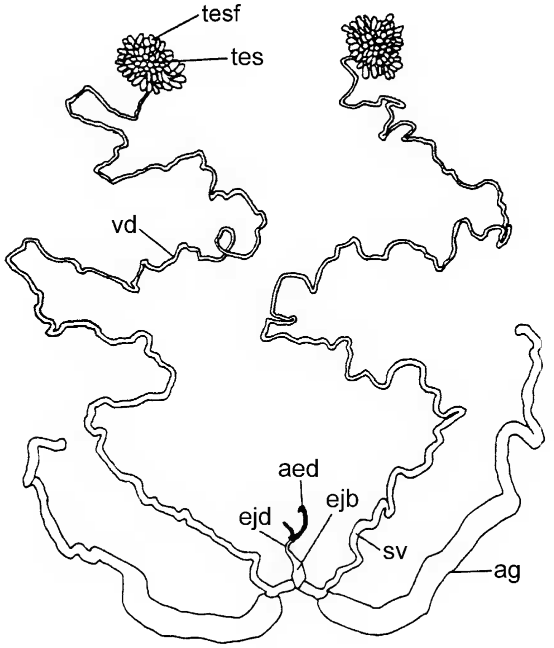

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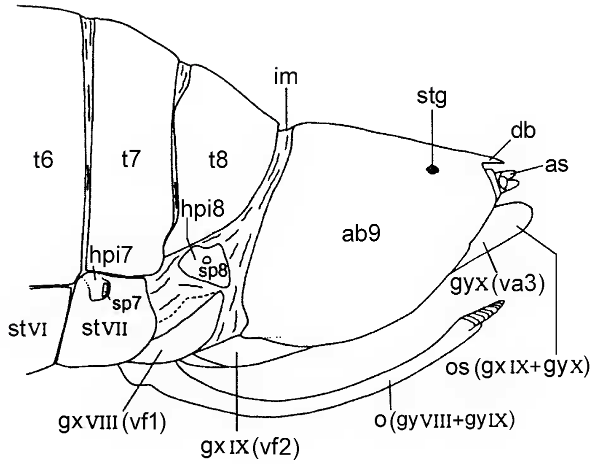
Figs. 25–26. Male genitalia and reproductive system: (Fig. 25) genitalia *in situ*, lateral view showing resting position of aedeagus and attachment of internal reproductive system, *Tamasa tristigma*, Cicadinae; (Fig. 26) reproductive system, full dissection, *Tamasa tristigma*, Cicadinae. Terminology adapted from Boulard (1996a) and Matsuda (1976). (*aed*) aedeagus; (*ag*) accessory gland; (*bp*) basal plate; (*ejb*) ejaculatory bulb; (*ejd*) ejaculatory duct; (*hpi 8*) hypopleurite 8; (*im*) intersegmental membrane; (*pyg*) pygofer; (*sp 8*) spiracle 8; (*st VII–VIII*) sternites VII and VIII; (*sv*) seminal vesicle; (*tes*) testis; (*tesf*) testicular follicles; (*t 8*) tergite 8; (*un*) uncus; (*vd*) vas deferens.



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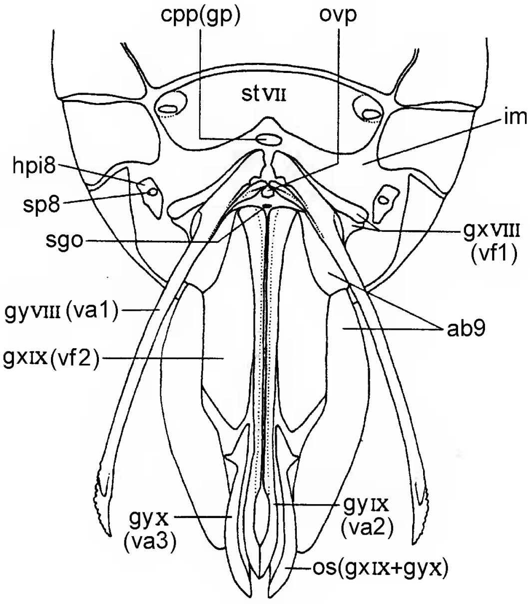

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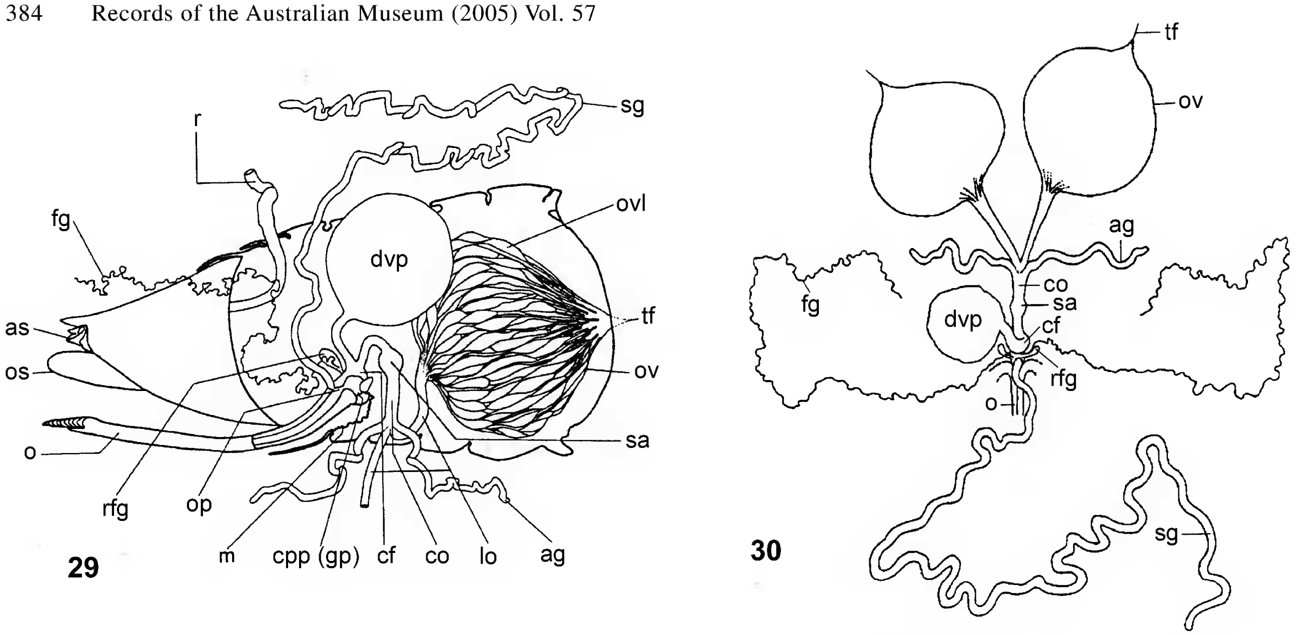
Figs. 27–28. Female terminalia, *Arunta perulata*, Cicadinae: (Fig. 27) lateral view with ovipositor free of sheath; (Fig. 28) ventral view with ovipositor divided exposing ovipore and orifice of spermathecal gland. Terminology adapted from Boulard (1996a). Terminologies in brackets are also in current use. (*ab 9*) abdominal segment 9 or tergite 9; (*as*) anal styles; (*cpp, gp*) copulapore, or gonopore; (*db*) dorsal beak; (*gx VIII–IX, vf 1–2*) gonocoxites VIII and IX or valvifers 1 and 2; (*gy VIII–X, va 1–3*) gonapophyses VIII, IX or X or valvulae 1, 2 or 3; (*hpi 7, 8*) hypopleurites 7 and 8; (*im*) intersegmental membrane; (*os*) ovipositor sheath (= gonocoxite IX + gonapophysis X); (*o*) ovipositor (= gonapophyses VIII + IX); (*ovp*) ovipore; (*sgo*) orifice of spermathecal gland; (*sp 7, 8*) spiracles 7 and 8; (*st VI, VII*) sternites VI, VII; (*stg*) stigma; (*t 6, 7, 8*) tergites 6, 7 or 8.



Figs. 29–30. Female reproductive system, *Arunta perulata*, Cicadinae: (Fig. 29) partial dissection, lateral view, nearside abdominal sclerites removed to expose reproductive system, carrefour and upper ovipositor cross-sectioned, nearside ovary and nearside filamentous gland and its reservoir removed; (Fig. 30) full dissection, dorsal view. Terminology after Boulard (1996a) and Duffels (1977). Terminology in brackets also in current use. (*ag*) accessory gland; (*as*) anal styles; (*cf*) carrefour; (*co*) common oviduct; (*cpp, gp*) copulapore, or gonopore; (*dvp*) dorsovaginal pouch; (*fg*) filamentous gland; (*lo*) lateral oviduct; (*m*) membrane; (*o*) ovipositor; (*op*) ovipore; (*os*) ovipositor sheath; (*ov*) ovary; (*ovl*) ovariole with eggs; (*r*) rectum; (*rfg*) reservoir of filamentous gland; (*sa*) seminal ampoule; (*sg*) spermathecal gland; (*st VII*) sternite VII; (*tf*) terminal filament of ovary.

HISTORICAL REVIEWS

Historical review of family classification

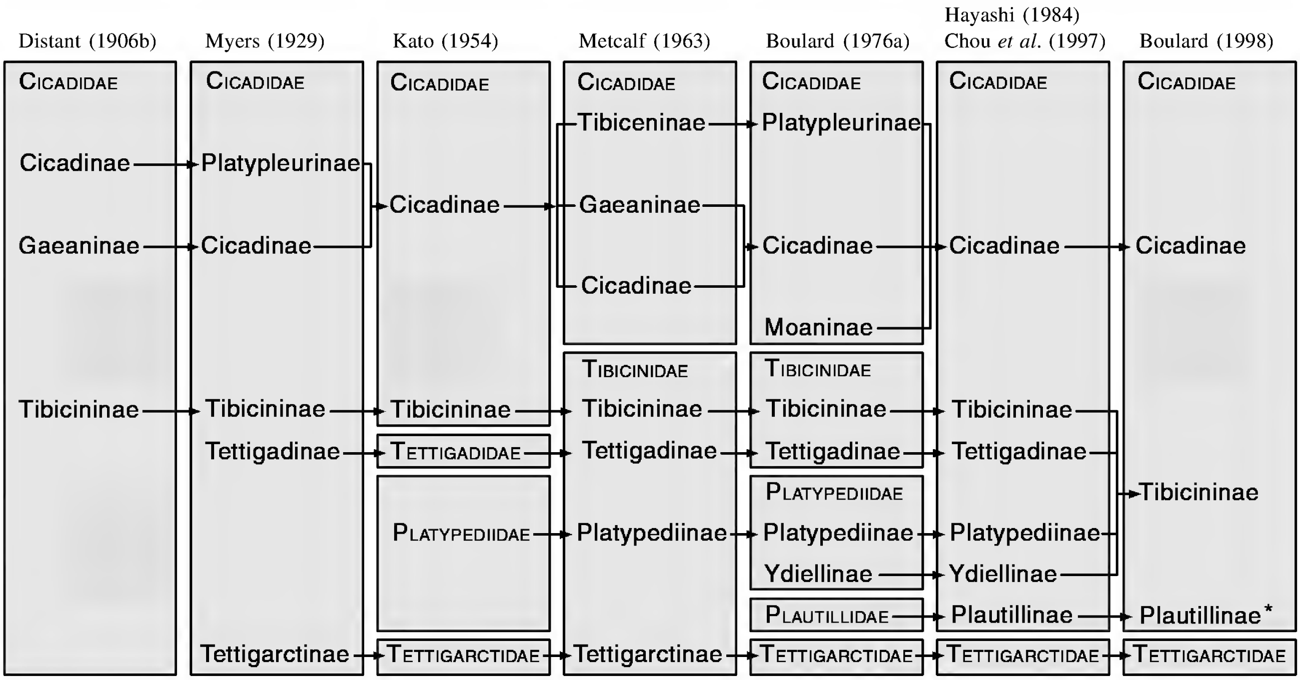
The cicadas were first recognized as a group (apart from a purely generic grouping) by Latreille (1825) when he erected the "family" Stridulantes, later to be formalized as the family Cicadidae (Westwood, 1840). Various other early terminologies and concepts were employed for subdividing both the Hemiptera and the Cicadidae (e.g., Amyot & Serville, 1843; Dohrn, 1859; Stål, 1866; Buckton, 1889) but many were not soundly based and consequently fell from favour. For example, Amyot & Serville (1843) proposed the first subfamily differentiation within the cicadas, founding two subfamilies, Reticelli and Octicelli, based on the presence or absence of reticulate venation on the fore wings, a condition that has arisen independently in at least three distinct branches of cicadas. The essence of some of these early concepts have been summarized by Westwood (1843: 33) and Buckton (1890).

In 1906 Distant published his *Synonymic Catalogue* of cicadas (Distant, 1906b), a comprehensive work documenting the world fauna, in which he employed a revised hierarchical classification for cicadas developed by him during preceding years (Distant, 1889, 1904a–c, 1905a–g). Distant divided the cicadas (family Cicadidae) into three subfamilies, Cicadinae, Gaeaninae and Tibicininae, based on the development of the timbal coverings. Subfamilies were further divided into 28 "Divisions" equivalent to tribes. This classification has remained the basis of modern cicada classifications.

The concept of a new name, the Tibiceninae, (as distinct from Distant's Tibicininae) was introduced by Van Duzee (1916) as a replacement for Distant's Cicadinae, brought about by a changeover in the type designation of the genus *Cicada* which led to the name Cicadinae being transferred to the subfamily Gaeaninae. This difference of one letter was to cause considerable future confusion. Distant had, in fact, previously used the spelling Tibiceninae (Distant, 1889) for those cicadas he later called Tibicininae (Distant, 1905b), and others have subsequently followed this error. Distant's Tibicininae is based on the genus *Tibicina* Amyot while Van Duzee based his Tibiceninae on the genus *Tibicen* Latreille. China (1964) and Boulard (1988a, 1998) have detailed much of the confusion caused and carefully explain the reasons, which are very complex. In particular, one should be aware that the tripartition of the Cicadidae into Tibiceninae, Cicadinae and Gaeaninae is completely erroneous in Metcalf's *Catalogue* (Metcalf, 1963), resulting from a mis-correlation of Metcalf's classification with that of Kato (1956) and other authors during the preparation of the catalogue after Metcalf's death in 1956.

Prior to the publication of Metcalf's *Catalogue*, Kato (1932) introduced an entirely new grouping for cicadas, the Platypediinae, which he later raised to family Platypediidae (Kato 1954); these were a small group of North American cicadas lacking timbals but possessing tympana. The only other entirely new grouping to be introduced since Distant (1906b) is the Plautillidae of Boulard (1975a) which is discussed in detail below.

An excellent overview of the development of the family/subfamily classification of cicadas since Distant (1906b) has been published by Hayashi (1984) and more recently updated by Chou *et al.* (1997) and here further updated to the present day (Fig. 31). Kato (1954) was the first to recognize more than just one family of cicadas, dividing them into four family groupings, the Tettigarctidae, Cicadidae, Tettigadidae and Platypediidae. Metcalf (1963), on the other hand, recognized only two, the Cicadidae and Tibicinidae. This disagreement on family rankings continues even today. The classification attaining the broadest acceptance is probably that of Hayashi (1984) who



* Boulard (1998) does not address the status of his former subfamilies Moaninae, Tettigadinae, Platypediinae and Ydiellinae, all placed in his family Tibicinidae. The Moaninae was shown to belong to the Dundubiini (Duffels, 1993). The remainder are assumed to have attained tribal ranking on changing the Tibicinidae to subfamily rank.

Fig. 31. Development of family and subfamily concepts for the Cicadoidea from the time of Distant's catalogue (1906b) to the most recently proposed classification (Boulard, 1998); modified from Hayashi (1984).

recognizes two families, the Tettigarctidae (containing one extant Australian genus of two species, and several fossil genera in the Mesozoic of the northern Hemisphere) and the Cicadidae (containing all other cicadas both extant and fossil), a conclusion also supported by Evans (1963), Moulds (1990) and Chou *et al.* (1997) and more recently by Boulard (1998). Within the Cicadidae Hayashi recognized six subfamilies, the Cicadinae, Tibicininae, Tettigadinae, Platypediinae, Ydiellinae and Plautillinae. Duffels (1993) also reviewed the higher classification of cicadas but the scope of his paper does not extend to a proposed classification but rather an evaluation of the families and subfamilies used in recent years. He did, however, believe that the Tettigarctidae are monophyletic and may be the sister group of the Cicadidae *sensu* Hayashi.

The most recent catalogue of cicadas (Duffels & van der Laan, 1985) distinguishes six families, following literature to 1980: the Cicadidae, Tibicinidae, Plautillidae, Platypediidae, Tettigadidae and Tettigarctidae. Their classification is essentially that of Boulard (1976b) and does not take into account developments since 1980.

Family classifications of Boulard & Hayashi

Some comments on the classifications of Boulard & Hayashi are warranted, both to assist an understanding of the differences between them and because the system of Boulard remains widely used today. These, and other cicada classifications, are primarily based on structures connected with the production of sound and related morphological structures, viz. timbals, timbal covers, tympana, and wing and genital stridulation mechanisms.

The families **Cicadidae** and **Tibicinidae** (more recently widely accepted as subfamilies Cicadinae and Tibicininae) are by far the largest groupings encompassing more than 95% of known species. These groupings are characterized by the possession of timbals, and the presence or absence of timbal covers respectively. Unlike Hayashi, Boulard (1976b) subdivided his Cicadidae into three, his subfamilies Platypleurinae, Cicadinae and Moaninae. The name Platypleurinae Schmidt, 1918, has been widely regarded as a junior synonym of Tibiceninae Van Duzee, 1916, and Duffels & van der Laan (1985) were justified in using Tibiceninae at that time. Boulard (1988a), however, provides detailed arguments for the justification of the name Platypleurinae over Tibiceninae and has retained Platypleurinae (Boulard, 1996a). Recently Duffels (1993) questioned Boulard's subdivision of his Cicadidae into Cicadinae and Platypleurinae. These groupings are based solely on the degree of development of the timbal covers, and as Duffels points out, apparently closely related genera are attributed to different subfamilies under this arrangement. Duffels also convincingly argued the sinking of Moaninae and this subfamily is now considered a part of the tribe Dundubiini of the Cicadinae.

Boulard (1973b, 1976a,b) took from the Tibicinidae five genera that lacked timbals, placing them as the **Platypediidae**. However, he recognized the relationships of these five genera to five diverse tribes of the Tibicinidae (Boulard, 1976b), and later (Boulard, 1986a, 1988a), conceding that the five genera were not a monophyletic group, he disbanded the family Platypediidae by distributing the genera between three subfamilies of the Tibicinidae: *Platypedia* and *Neoplatypedia* to the Platypediinae, *Ydiella* (= *Maroboduus* Distant) to Ydiellinae, and *Karenia* and *Lamotialna* to the Tibicininae. Boulard appeared unaware at the time that

Hayashi (1984) had recognized similar concepts for the Platypediinae and Ydiellinae four years earlier as he made no mention of Hayashi's work in this regard. The downgrading of the Platypediidae to subfamily ranking by Hayashi (1984) apparently occurred too late for incorporation in the catalogue of Duffels & van der Laan (1985).

The **Plautillidae** was established by Boulard (1975a) to accommodate the genus *Plautilla* Stål. The genus includes just three species from South America. While Duffels & van der Laan (1985) recognized the Plautillidae at family rank, Duffels (1993) questioned this ranking pointing to the need for a phylogenetic analysis of *Plautilla* relationships. Hayashi (1984) retained the group at subfamily rank and, like Boulard (1975a), discussed possible relationships with *Zammara* Amyot & Serville.

Boulard (1976a, 1988a) places the **Tettigadinae** as a subfamily of Tibicinidae because these cicadas lack timbal covers, but Duffels & van der Laan (1985) recognize them at family rank following China (1964). As Duffels (1993) points out, the monophyly of *Tettigades* and allied genera is suggested by the broad head and very small eyes, but he emphasizes the need for further phylogenetic analysis of this group. Hayashi (1984) places the group at subfamily rank, but because he does not recognize the family Tibicinidae, the question of the direct linking of Tettigadinae with Tibicininae does not arise.

The name **Tettigarctidae** originates from Distant's Division Tettigarctaria and the Tettigarctidae are now widely accepted at family rank, and mostly so as the sister group of all other cicadas (Hayashi, 1984; Moulds, 1990; Duffels, 1993; Chou *et al.*, 1997; Boulard, 1998).

It is important to note that Boulard (1998) now agrees that the cicadas are best divided into only two families, the Tettigarctidae and Cicadidae, with all other rankings subordinate. He mentions three subfamilies, Cicadinae, Tibicininae (his former Tibicinidae) and Tettigarctinae but the status of groups such as Plautillidae and Tettigadidae is not addressed.

Infraorder concepts for cicadas

Finally, brief mention is made of some higher categories of hemipteran classification that relate to the systematic position of cicadas and are currently in use. The superfamily **Cicadoidea** (Metcalf, 1939; Evans, 1956) unifies the cicada families, both extant and fossil. Lameere (1935) and Evans (1946, 1951), developed the infraorder concept for cicadas; they fall within **Cicadomorpha**, a category encompassing the Cicadoidea, Cercopoidea and the synonymous Membracoidea/Cicadelloidea (Evans, 1963; Hamilton, 1981; Carver *et al.*, 1991; Blocker, 1996). The group **Auchenorrhyncha** (Duméril, 1806) (= Cicadariae Latreille) encompasses the Cicadomorpha plus Fulgoromorpha but the validity of this grouping as a monophyletic concept has been challenged (Hamilton 1981, 1996; Sorensen *et al.*, 1995); some authors give the Auchenorrhyncha subordinal rank (e.g., Carver *et al.*, 1991) while others place it immediately subordinate to the suborder Homoptera as a "Series" (e.g., Richards & Davies in Imms, 1957). The term **Rhynchota** now receives little recognition but was widely employed in the past, especially by Distant; it is mostly considered an Order ranking synonymous with Hemiptera. Boulard (1996a) provides further comments on each of these groupings and a detailed historical account for each.

Historical review of tribal classification

The Cicadidae/Cicadinae and Tibicinidae/Tibicininae have been traditionally divided into tribes. This tribal classification, for the most part, was developed by Distant (1906b). Distant recognized 28 Divisions (i.e. tribes) but J.G. Myers (1929) accepted only five of these, the Chlorocystini, Hemidictyini and Tibicinini placed in the subfamily Tibicininae and Moganniini and Cicadini in the subfamily Cicadinae. However, J.G. Myers was alone in his rejection of Distant's tribal groupings. Kato (1932) recognized all but three of Distant's Divisions (Lahugadaria, Hamzaria and Cicadatraria); of the others he retained 23 at tribal rank and transferred two to subfamily rank following Jacobi (1907b) and Tillyard (1926) (Tettigadesaria and Tettigarctaria respectively). He also introduced two new tribes (Dazini and Prasiini) and four new subtribes of the Dundubiini as well as recognizing the Platypleurini and Talaingini of Schmidt (1919). Kato (1932) was also the first to provide a key to tribes.

The tribal categories used by Kato (1932) were retained by him in his subsequent publications (e.g., Kato, 1954, 1956). The latter work (Kato, 1956) contains the most recently published comprehensive key to tribes available. Metcalf (1963) adopted Kato's tribal classification but added one additional tribe (Platylomiini, Metcalf, 1955) and six additional subtribes of which only the Tibicenaria (Metcalf, 1963) postdates Kato (1932).

Duffels & van der Laan (1985) follow Metcalf's classification closely as their catalogue was a supplement to Metcalf's work; they do, however, update tribal groupings to follow literature to 1980. The Tibicenini loses its subtribes and the Dundubiini loses one subtribe, all a consequence of the Cryptotympanaria attaining tribal status with three subtribes, Heteropsaltriaria from the Dundubiini and two that are new (Boulard, 1979b); the new tribes Distantadini, Oncotympanini and Gymnotympanini are added (Orian, 1963; Ishihara, 1961, and Boulard, 1979a, respectively); the subtribe Hamzaria is raised to tribal rank (Esaki & Miyamoto, 1975); the family Platypediidae, subfamily Platypediinae, is allocated three tribes all of which are new (Boulard, 1975b, 1976b); the Plautillini attains family rank; and Platylomiini is no longer recognized on account of its synonymy with Dundubiini (Duffels, 1977).

The tribes and subtribes used today remain essentially those catalogued by Duffels & van der Laan; none has been added since 1980 but Lee & Hayashi (2003) amalgamated the tribes Cicadini and Dundubiini and included in the subtribe Cicadina the subtribes Terpnosiina and Leptopsaltriina. The contribution of Distant to the classification we use today is considerable. Of the 35 tribes and subtribes recognized more than half originate from Distant's classification (Distant, 1906b); only one of his 28 "Divisions", the Cicadatraria, is no longer recognized. Australian cicada species currently fall within 12 of these tribes and two subtribes (Moulds, 1990).

OVERVIEW OF FAMILY-GROUP CONCEPTS, PAST AND PRESENT

Below I document current and former family-group concepts in detail in an attempt to clarify misunderstandings relating to definitions and nomenclature. All previously proposed families and subfamilies are examined, plus all tribal concepts that have either been directly associated with the Australian cicada fauna or those that I consider likely to be so. Diagnoses have been taken solely from the published literature, both from former diagnoses and characters presented in keys.

A review of some previously proposed phylogenies for cicadas is also provided and an evaluation of extant family-group classifications is included.

Family and subfamily groupings

Current family and subfamily classifications are largely based upon sound-producing mechanisms and the morphological structures associated with these mechanisms (Distant, 1906b; Kato, 1956; Boulard, 1976a, 1988a; Hayashi, 1984; Chou *et al*., 1997).

The current broad consensus is for a family/subfamily classification consisting of two families, Tettigarctidae with subfamilies Tettigarctinae and Cicadoprosbolinae, and Cicadidae with 5 or 6 subfamilies, *viz*. Cicadinae, Tibicininae, Tettigadinae, Ydiellinae, Plautillinae and possibly Platypediinae (Hayashi, 1984; Moulds, 1990; Chou *et al*., 1997; Boulard, 1998). However, there is also in use a classification comprising four families, Tettigarctidae, Plautillidae, Cicadidae with two subfamilies Cicadinae and Platypleurinae, and Tibicinidae with four subfamilies Tibicininae, Tettigadinae, Platypediinae and Ydiellinae (Boulard, 1988a, 1996a); Duffels & van der Laan (1985) follow the latter but place Tettigadinae at family rank (see Historical Review of Family Classification, p. 384).

Distant (1906b), Kato (1956), Boulard (1988a) and Chou *et al*. (1997) provide keys to their family/subfamily classifications.

Not only is there disagreement among systematists concerning recognition of family/subfamily rankings, there is also a lack of consensus concerning the nomenclature and authority of some categories. I address the latter problems below.

The following family and subfamily rankings are those that have been used with varying degrees of acceptance since Boulard (1976a) proposed his comprehensive review of cicada higher classification. Each ranking is defined together with an overview of its current status. Generic names in **bold print** are genera not found in Australia.

Cicadidae/Cicadinae Latreille, 1802

Type genus. *Cicada* L. (type species *Cicada orni* L.).

Included genera. Treated at family rank all Cicadoidea except Tettigarctidae (*sensu* Hayashi, 1984; Moulds, 1990). Treated at subfamily rank there are two concepts: (1) *Anapsaltoda* Ashton, *Arenopsaltria* Ashton, *Arunta* Distant, *Cicada* L., *Cosmopsaltria* Stål, *Cryptotympana* Stål, *Cyclochila* Amyot & Serville, *Diceropyga* Stål, *Dundubia* Amyot & Serville, *Henicopsaltria* Stål, *Illyria* Moulds, *Lyristes* Horváth, *Macrotristria* Stål, *Neopsaltoda* Distant, *Oxypleura* Amyot & Serville, *Psaltoda* Stål, *Tamasa* Distant, *Thopha* Amyot & Serville, and many other genera with timbal covers present (*sensu* Hayashi, 1984; Moulds, 1990); (2) *Cicada, Cyclochila, Cosmopsaltria, Diceropyga, Dundubia, Illyria, Tamasa* and other genera which have timbal covers only partly developed (for the converse, those with fully developed timbal covers, see Platypleurinae below) (*sensu* Boulard, 1976a).

Distribution. Cosmopolitan.

Diagnosis. Timbal covers present, partly or completely covering timbals and metanotum entirely concealed under cruciform elevation (Hayashi, 1984; Moulds, 1990); or, timbal covers present but only partly covering timbals (Boulard, 1976a).

Discussion. Boulard (1988a, 1996a, 1998) implies that family-group names based on *Cicada* L. date from Latreille (1802: 257) who designated the true cicadas the "*Cicadae verae*", based upon *Cicada orni*, in contrast to the rest of the "Cicadariae" (= Auchenorrhyncha). While the *Code* does not specifically state that a family-group name must be derived from a single word it clearly implies that should be the case. However, if we reject Latreille's *Cicadae verae* on that basis, the family-group names based on *Cicada* still originate from Latreille (1802). In this publication Latreille also introduces the name "*Cicadariae*", which he nominates at family ranking, describes, and in which he incorporates the "*Cicadae verae*" where *Cicada orni* L. is listed as the sole example. Although Latreille's family concept was far broader than what we consider cicadas to be today (his concept extended to what we now call Auchenorrhyncha) his designation clearly fulfils the requirements of the *Code* for a family-group name based on *Cicada* L. with type species *Cicada orni* L.

The designation of other authorities (e.g., Leach, 1815; Westwood, 1840) by other authors are incorrect; they either post-date Latreille and also contravene Article 36.1 of the *Code*, or the arguments presented are misleading (e.g., China, 1964: 155).

Moaninae Boulard, 1976

Boulard established this subfamily to accommodate the single species *Moana expansa* J.G. Myers. Having acquired further material of *M. expansa*, Duffels (1993) was able to provide convincing arguments for the disbanding of the Moaninae, placing *Moana* within the tribe Dundubiini, subtribe Cosmopsaltriina, together with three additional species of *Moana* transferred from *Aceropyga* Duffels. *Moana* has not been included in my study as there is no reason to doubt Duffels" assessment which is based on strong synapomorphies well supported by cladistic analysis.

Platypediidae/Platypediinae Kato, 1932

Type genus. *Platypedia* Uhler (type species *P. areolata* Distant).

Included genera. *Platypedia* Uhler, *Neoplatypedia* Davis (*sensu* Boulard, 1986a, 1988a; Duffels, 1993).

Distribution. North America.

Diagnosis. Males lack functional timbals and accessory stridulatory organs (calling is by clapping the fore wings); uncal lobe of male genitalia extends caudad (Boulard, 1996a; Hayashi, 1984).

Discussion. Duffels (1993) believes that Boulard (1986a, 1988a) was correct in disbanding the family Platypediidae by distributing the five included genera to three subfamilies of the Tibicinidae "since the different genera probably lost their timbal organs independently". The two closely allied genera listed above are widely recognized as forming the subfamily Platypediinae. Chou *et al.* (1997) appeared to have been unaware of the break up of the Platypediidae and have followed Boulard's original broader concept (by including *Karenia* Dist.) although treating it at subfamily rather than family rank.

Platypleurinae Schmidt, 1918

Type genus. *Platypleura* Amyot & Serville (type species *P. stridula* L.).

Included genera. *Anapsaltoda* Ashton, *Arunta* Distant, *Cosmopsaltria* Stål, *Cryptotympana* Stål, *Diceropyga* Stål, *Dundubia* Amyot & Serville, *Henicopsaltria* Stål, *Lyristes* Horváth (= *Tibicen* Latreille), *Macrotristria* Stål, *Neopsaltoda* Distant, *Oxypleura* Amyot & Serville, *Platypleura* Amyot & Serville, *Psaltoda* Stål, *Thopha* Amyot & Serville, and many other genera where the males have full development of the timbal covers (*sensu* Boulard, 1976a).

Distribution. Cosmopolitan.

Diagnosis. Males with complete development of the timbal covers (as distinct from partial development, see Cicadidae/ Cicadinae above) (Boulard, 1976a).

Discussion. The name Platypleurinae Schmidt, 1918, has been widely recognized as a junior synonym of Tibiceninae. However, following the arguments presented under "Tibiceninae" below, Tibiceninae and its family-group name derivatives completely change their meaning because of a correction to the type species of *Tibicen*. Following Boulard's argument (Boulard, 1988a, 1998, 2001) Tibiceninae falls as an objective junior synonym of Tibic~~in~~inae. The name Platypleurinae thus replaces Tibiceninae as used in its former context. This matter does not arise for those authors who do not recognize the subdivision of the Cicadidae into Platypleurinae and Cicadinae, i.e. cicadas with complete or incomplete timbal covers respectively (Hayashi, 1984; Moulds, 1990; Lee, 1995; Chou *et al.*, 1997).

Schmidt (1918) established the tribe Platypleurini and following Article 36.1 of the *Code* any subsequent family-group ranking of it should retain the original author and date; alternate authorities appearing in the literature are erroneous. The authority "Mijers" listed by Duffels & van der Laan (1985) is a typographical error, "Myers" was intended.

Plautillidae/Plautillinae Distant, 1905

Type genus. *Plautilla* Stål (type species *P. stalagmoptera* Stål).

Included genera. *Plautilla* Stål (*sensu* Boulard, 1975a).

Distribution. South America (Ecuador and Colombia).

Diagnosis. Males with timbal covers emanating from metanotum; reduction of vannal region of hind wings; accessory sound-producing mechanism present on anterolateral corner of mesonotum; male sternites III–VI completely membranous (Boulard, 1975a; Hayashi, 1984).

Discussion. Distant (1905h) established this family-group name (as the Division Plautillaria) and following Article 36.1 of the *Code* any subsequent family-group ranking of it should retain the original author and date; alternate authorities appearing in the literature are erroneous.

Tettigadidae/Tettigadinae Distant, 1905

Type genus. *Tettigades* Amyot & Serville (type species *Tettigades chilensis* Amyot & Serville).

Included genera. *Acuticephala* Torres, *Alarcta* Torres, *Babras* Jacobi, *Calliopsida* Torres, *Chonosia* Distant, *Coata* Distant, *Mendozana* Distant, *Psphenotettix* Torres, *Subpsaltria* Chen, *Tettigades* Amyot & Serville (*sensu* Duffels & van der Laan, 1985; Chou *et al.*, 1997).

Distribution. China, North and South America.

Diagnosis. Males with timbals present but timbal covers absent; mesonotal accessory stridulatory apparatus present, comprising a mesonotal file and plectrum at the base of fore wing vein CuA; a broad head and very small eyes (Distant, 1905d; Jacobi, 1907b; Chen, 1943; Boulard, 1976a, 1986b; Hayashi, 1984; Duffels, 1993; Chou *et al.*, 1997).

Discussion. Distant (1905d) established this family-group name (as his Division Tettigadesaria) and following Article 36.1 of the *Code* the original author and date are to be retained for any subsequent ranking; alternate authorities appearing in the literature are erroneous. Only Chen (1943) and Chou *et al.* (1997) include the Chinese genus *Subpsaltria* here; Liu (1978) excludes *Subpsaltria* from his review of the Chinese Cicadidae. Other authors place *Subpsaltria* in the Tibicinidae, Tibicinini.

Tettigarctidae Distant, 1905

Type genus. *Tettigarcta* White (type species *T. tomentosa* White).

Included genera. *Tettigarcta*; plus the following fossil genera: *Architettix* Hamilton, *Cicadoprosbole* Bekker-Migdisova, *Elkinda* Shcherbakov, *Eotettigarcta* Zeuner, *Hylaeoneura* Lameere and Severin, *Involuta* Zhang, *Liassocicada* Brodie, *Liassotettigarcta* Nel, *Meuniera* Piton, *Paraprosbole* Whalley, *Protabanus* Hong, *Shuraboprosbole* Bekker-Migdisova, *Tettigambra* Shcherbakov, *Turutanovia* Bekker-Migdisova (*sensu* Nel, 1996; Shcherbakov, 1996, in prep.).

Distribution. Australia (extant), Northern Hemisphere (fossil).

Diagnosis. Males and females with functional but very small timbals; tympana absent; abdominal resonant cavity absent; fore wing radial posterior (RP) arising closer to wing base than to node, veins CuP, 1A, 2A and 3A separated; nervous system with thoracic ganglia separated; male genitalia with styles; tarsal empodia present; pronotum greatly expanded concealing much of mesonotum (Evans, 1941; Moulds, 1990).

Discussion. The only two extant species in this family, *Tettigarcta crinita* and *T. tomentosa*, in large part provide the family characterization. Characters from fossil genera consolidate characterizations but do not provide additional characters.

Boulard & Nel (1990) and Shcherbakov (in prep.) have divided the Tettigarctidae (one extant and 14 fossil genera) into two subfamilies, the Tettigarctinae comprising the Recent

Tettigarcta and Cenozoic *Eotettigarcta* and *Meuniera*, and the Cicadoprosbolinae comprising all the Mesozoic genera. Shcherbakov suggests that the more specialized nymphal chaetotaxy and the nymphal labium position similar to that of Cicadidae (evaluated from the single known fossil tettigarctid nymph, *Tettigambra mouldsi* Shcherbakov) may indicate that the Cicadidae descended from the Cicadoprosbolinae rather than the Tettigarctinae, an idea also suggested by Bekker-Migdisova (1947) based upon wing evidence.

Distant (1905g) established this family-group name (as his Division Tettigarctaria) and following Article 36.1 of the *Code* the original author and date are to be retained for any subsequent ranking; alternate authorities appearing in the literature are erroneous.

Tibiceninae Van Duzee, 1916

Type genus. *Tibicen* Latreille, 1825 (type species *Cicada plebeja* Scopoli, *non* L. [but see discussion below]).

Included genera. *Anapsaltoda* Ashton, *Arunta* Distant, *Cosmopsaltria* Stål, *Cryptotympana* Stål, *Diceropyga* Stål, *Dundubia* Amyot & Serville, *Henicopsaltria* Stål, *Lyristes* Horváth (= *Tibicen* of some authors), *Macrotristria* Stål, *Neopsaltoda* Distant, *Oxypleura* Amyot & Serville, *Platypleura* Amyot & Serville, *Psaltoda* Stål, *Thopha* Amyot & Serville, and many other genera where the males have full development of the timbal covers (*sensu* Boulard, 1976a).

Distribution. Cosmopolitan.

Diagnosis. Males with *complete* development of the timbal covers (as distinct from partial development, see Cicadidae/Cicadinae, p. 387).

Discussion. This is a subfamily concept no longer accepted where the timbal covers completely, rather than only partly, cover the timbals. Boulard (1988a, 1998, 2001) has provided a detailed argument for the suppression of the name Tibiceninae in favour of Platypleurinae (see also discussion under Platypleurinae, p. 388).

Because *Tibicen* and *Tibicina* have now been found to share the same type species (*Cicada haematodes* Scopoli, see discussion under "Tibicenini", p. 393), *Tibicina* falls as an objective junior synonym of *Tibicen*. However, like *Tibicen, Tibicina* is also the type genus of a suite of family-group taxa. Thus, the family-group names based upon *Tibicen* and *Tibicina* become objective synonyms. However, the oldest of these family-group names, i.e. those based on *Tibicina*, take priority (Article 23.3).

The one letter difference between the family-group names derived from *Tibicen* and those derived from *Tibicina* (for example Tibiceninae and Tibicininae) has caused considerable confusion and a plethora of errors in cicada systematics. China (1964) and Boulard (1988a, 1998, 2001) list and discuss many of the major errors that perpetuate misunderstandings, e.g., the utter confusion in the family/subfamily classification of Metcalf's catalogue (Metcalf, 1963).

This one letter difference in family-group name and the complete reversal in concept of the Tibiceninae (to the same as that of the Tibicininae; see discussion under "Tibicenini", p. 393), has led Boulard (1988a, 1998, 2001) to recommend the complete abandonment of *Tibicen* and its associated family-group names. Suppression requires a ruling from the International Commission of Zoological Nomenclature but this has not been forthcoming.

Tibicinidae/Tibicininae Distant, 1905

Type genus. *Tibicina* Amyot, 1847 (type species *Cicada haematodes* Scopoli).

Included genera. All genera that have males with developed timbals but timbal covers absent. These comprise the majority of described genera within Cicadoidea.

Distribution. Cosmopolitan.

Diagnosis. Males with developed timbals but timbal covers absent (Distant, 1905b; Kato, 1954; Boulard, 1976a, 1996a; Hayashi, 1984; Moulds, 1990; Chou *et al*., 1997).

Discussion. The authorship of this family-group name has been attributed to Buckton (1889) by some authors (e.g., Metcalf, 1963). Boulard (1988a, 1998) points out that Buckton's designation is invalid as he gives neither a diagnosis nor an accompanying genus.

The one letter difference between the family-group names derived from *Tibicina* and those derived from *Tibicen* (for example Tibicinidae and Tibicenidae) has caused considerable confusion and a plethora of errors in cicada systematics. See also Tibiceninae above for further discussion.

Ydiellinae Boulard, 1973

Type genus. *Maroboduus* Distant (=*Ydiella* Boulard) (type species *Maroboduus fractus* Distant).

Included genera. *Maroboduus* (after Boulard, 1973b, 1976a, 1986a, 1988a).

Distribution. Two species only, from West Africa.

Diagnosis. Males lack timbals; stridulatory apparatus between fore and hind wings in vicinity of the wing coupling (Boulard, 1973b, 1976a, 1986a,b).

Discussion. Originally placed as a subfamily of the Platypediidae (Boulard, 1973b), but on disbanding the Platypediidae *q.v*., the Ydiellinae were considered a subfamily of the Tibicinidae (Boulard, 1988a). Later, Boulard (1993) reassessed the phylogenetic position of *Maroboduus*, and reduced the Ydiellinae to subtribal rank, Ydiellaria within the tribe Gymnotympanini. As Gymnotympanini is now considered a junior synonym of Chlorocystini (Boer, 1995b) and *Maroboduus* is excluded, Ydiellaria is considered best placed at tribal ranking as the Ydiellini **n.stat.** Boulard (1988a) placed *Ydiella* as a junior synonym of *Maroboduus* (see above) but correctly retained the family-group name Ydiellinae following Article 40.1 of the *Code* (4th edition).

Tribal groupings for Australian cicadas

Some 35 tribes are recognized worldwide. The Australian cicadas currently fall within 11 of these, 10 in the family Cicadidae (*sensu* Hayashi, 1984; Moulds, 1990), plus another in the family Tettigarctidae where no tribes are allocated (Duffels & van der Laan, 1985; Moulds, 1990; Boer, 1995b). Six of the 10 tribes of Australian Cicadidae fall within the subfamily Cicadinae and four within Tibicininae. This is essentially the classification of Distant (1906b) except for the addition of the Platypleurini Schmidt, 1918 and Prasiini Matsumura, 1917. Current tribal placements for Australian genera have been summarized by Moulds (1990). Two tribes are endemic, Cyclochilini and Thophini, while the remainder are widespread through the Oriental region with the majority extending far beyond.

Tribal definitions have largely remained ill-defined, often little unchanged since Distant's time (Distant, 1906b). Diagnoses given below are derived from the published literature, including characters given in keys. Where definitions have changed over time a consensus from the most recent publications has been adopted.

Kato (1956) provides the most comprehensive key to tribes, incorporating the 27 tribes as then known. Keys to tribes for regional faunas are provided by Liu (1978), Kato (1961) and Boulard (1996a) but each presents a narrow focus from a worldwide perspective.

Chlorocystini Distant, 1905

Type genus. *Chlorocysta* Westwood (type species: *C. vitripennis* Westwood).

Included genera. *Aedeastria* Boer, *Baeturia* Stål, *Chlorocysta* Westwood, *Cystopsaltria* Goding & Froggatt, *Cystosoma* Westwood, *Glaucopsaltria* Goding & Froggatt, *Guineapsaltria* Boer, *Gymnotympana* Stål, *Mirabilopsaltria* Boer, *Owra* Ashton, *Papuapsaltria* Boer, *Scottotympana* Boer, *Thaumastopsaltria* Stål, and *Venustria* Goding & Froggatt (*sensu* Boer, 1995b).

Distribution. Oriental and Australian regions.

Diagnosis. Timbal covers absent; fore wing with a very narrow hind margin; pronotum medially furrowed; cruciform elevation very narrow; male abdomen inflated or dilated with central longitudinal dorsal ridge; a reduced or absent medial uncal lobe; aedeagus S-shaped; a ventrally angularly swollen postclypeus (Boer, 1995b). The single apomorphy uniting the tribe is the male's S-shaped aedeagus.

Discussion. The tribe has been reviewed by Boer (1982, 1986, 1989, 1990, 1991, 1992a,b, 1993a,b, 1994a,b, 1995a,b, 1997). Boer (1995b) synonymized the Gymnotympanini with the Chlorocystini. In the same paper he also transferred to the Chlorocystini the two Australian genera then placed in Hemidictyini, viz. *Cystosoma* and *Cystopsaltria*.

Cicadettini Buckton, 1889

Type genus. *Cicadetta* Amyot (type species: *Cicada montana* Scopoli).

Included genera. *Amphipsalta* Fleming, *Birrima* Distant, *Buyisa* Distant, *Cicadetta* Amyot, *Cicadivetta* Boulard, *Curvicicada* Chou & Lu, *Euryphara* Horváth, *Fijipsalta* Duffels, *Froggattoides* Distant, *Hilaphura* Webb, *Kikihia* Dugdale, *Kobonga* Distant, *Leptopsalta* Kato, *Linguacicada* Chou & Lu, *Maoricicada* Dugdale, *Melampsalta* Kolenati, *Mouia* Distant, *Myersalna* Boulard, *Notopsalta* Dugdale, *Pagiphora* Horváth, *Pauropsalta* Goding & Froggatt, *Pinheya* Dlabola, *Poviliana* Boulard, *Rhodopsalta* Dugdale, *Saticula* Stål, *Scolopita* Chou and Lei, *Stellenboschia* Distant, *Takapsalta* Matsumura, *Tettigetta* Kolenati, *Tibeta* Lei & Chou, *Urabunana* Distant, *Xossarella* Boulard (*sensu* Metcalf, 1963; Duffels & van der Laan, 1985; Boulard, 1988c, 1996a, 1997; Boulard & Nel, 1990, Chou *et al*., 1997).

Distribution. All faunal regions except the Neotropics.

Diagnosis. Timbal covers absent; pronotal lateral margin not developed or dilated; head not markedly small; fore wings hyaline, median and cubitus anterior veins fused or coalesced and leaving the basal cell together from a single apex to the basal cell; aedeagus small, divided into three lobes (Singh-Pruthi, 1925; Kato, 1956; Boulard, 1996a).

Discussion. Boulard (1988a, 1998) and Moulds (1988) detail reasons why *Cicada montana* is the type species of *Cicadetta*. The past confusion concerning the generic names *Cicadetta* and *Melampsalta* has led to confusion regarding a choice between the tribal names Cicadettini and Melampsaltini. Again, Boulard (1988a, 1998) and Moulds (1988) provide reasons for the selection of Cicadettini. Further, the authorship of Cicadettini dates from Buckton (1889), and not Buckton (1890) as generally quoted (Boulard, 1988a, 1998).

Cicadini Latreille, 1802

Type genus. *Cicada* L. (type species: *Cicada orni* L.).

Included genera. *Cicada* L., *Cicadatra* Kolenati, *Emathia* Stål, *Illyria* Moulds, *Leptosemia* Matsumura, *Neocicada* Kato, *Nipponosemia* Kato, *Onomacritus* Distant, *Psalmocharias* Kirkaldy, *Tamasa* Distant, *Taungia* Ollenbach, *Triglena* Fieber, *Vagitanus* Distant (*sensu* Metcalf, 1963; Duffels & van der Laan, 1985).

Distribution. Cosmopolitan.

Diagnosis. Timbal covers partly covering timbal cavity, rounded anteriorly, not angulate; head including eyes wider than base of mesonotum; lateral margin of pronotum not ampliate; fore and hind wings hyaline, sometimes maculate; male opercula short and transverse; male sternites often thin in part (Distant, 1906a, 1912; Kato, 1956, 1961; Liu, 1978).

Discussion. Lee & Hayashi (2003) amalgamated the Cicadini with the Dundubiini but gave no reasons for doing so (see discussion under Dundubiini, p. 391).

Boulard (1988a, 1998) shows that all family-group names based on *Cicada* L. date from Latreille (1802). For a full discussion of this matter see "Cicadidae/Cicadinae", p. 387. The designations of other authorities (e.g., Distant, 1905 and Oshanin, 1907) by other authors are incorrect; they post-date Latreille and also contravene Article 36.1 of the Code.

Cryptotympanini Handlirsch, 1925

Type genus. *Cryptotympana* Stål [type species: *Tettigonia atrata* F. = *C. pustulata* (F.)].

Included genera. *Anapsaltoda* Ashton, *Antankaria* Distant, *Cacama* Distant, *Chremistica* Stål, *Cornuplura* Davis, *Cryptotympana* Stål, *Diceroprocta* Stål, *Heteropsaltria* Jacobi, *Lyristes* Horváth, *Macrotristria* Stål, *Neopsaltoda* Distant, *Nggeliana* Boulard, *Orialella* Metcalf, *Psaltoda* Stål, *Raiateana* Boulard, *Salvazana* Distant (*sensu* Boulard, 1979b; Hayashi, 1987; includes Lyristini, see discussion below).

Distribution. All faunal regions but absent from continental Africa.

Diagnosis. Timbals entirely concealed by timbal covers, the timbal covers meeting or leaving a narrow gap with the opercula; fore and hind wings hyaline or partly coloured; head broad, at least as wide of the base of the mesonotum;

no paranota on the pronotum; uncus undivided, short or very short, round at apex and without hamuliform differentiation; females ditrysian but ovipore and copulapore very close (Boulard, 1979b).

Discussion. Boulard (1979b) combined the Lyristini with the Cryptotympanini believing that they represented a single monophyletic group. Subsequent authors have followed this arrangement except Duffels & van der Laan (1985). Boulard (1979b) recognized three subtribes of the Cryptotympanini, the Cryptotympanaria, Heteropsaltriaria and Nggelianaria, based upon the length of fore wing cells and whether the timbal covers meet the opercula, but he did not allocate genera to these subtribes apart from the type genus of each. Duffels & van der Laan (1985) followed Boulard's subtribal arrangement, but as mentioned above, they excluded the Lyristini. Authors taking the broader perspective for the tribe have not attempted subtribal division.

There has been a lack of consensus on which of the two tribal names, Lyristini or Cryptotympanini, should apply to the broader concept. Boulard (1979b) correctly used the older of the two names, Cryptotympanini, but later (Boulard, 1988a) he adopted Lyristini (as well as Lyristinae). More recently he has again correctly used Cryptotympanini (Boulard, 1996a). Only Chou *et al.* (1997) have incorrectly maintained the name Lyristini for this broader tribal concept.

However, Boulard (1998: 117, 2001) now appears to have amalgamated the Cryptotympanini within the Platypleurini by placing the type species of *Cryptotympana, C. atrata* (F.), in the subtribe Cryptotympanina of the tribe Platypleurini but no explanation for this new arrangement was provided.

Cyclochilini Distant, 1904

Type genus. *Cyclochila* Amyot & Serville (type species: *Tettigonia australasiae* Donovan).

Included genera. *Arenopsaltria* Ashton, *Cyclochila* Amyot & Serville, *Henicopsaltria* Stål, (after Metcalf, 1963; Duffels & van der Laan, 1985; Hayashi, 1987; Moulds, 1990).

Distribution. Australia.

Diagnosis. Timbal covers completely covering timbal cavity; fore wings hyaline; lateral part of pronotum dilated; abdomen broad, medially widened and distinctly abbreviated posteriorly, in male (principally) abdomen obliquely depressed on each side, its greatest width almost twice that of head between eyes, male 2nd and 3rd abdominal segments large and about half length of abdomen; opercula not extending beyond base of metasternum (Distant, 1904a, 1912; Kato, 1956).

Discussion. Hayashi (1987) considered the genera "*Psaltoda, Macrotristria* … etc." as belonging to the Tibicenini (= Cryptotympanini). Hence *Psaltoda, Macrotristria* plus the two genera closely allied to *Psaltoda, Anapsaltoda* and *Neopsaltoda*, are placed above in Cryptotympanini.

Dundubiini Atkinson, 1886

Type genus. *Dundubia* (type species: *Tettigonia vaginata* F.).

Included genera. *Aceropyga* Duffels, *Aola* Distant, *Ayesha* Distant, *Ayuthia* Distant, *Basa* Distant, *Brachylobopyga* Duffels, *Calcagninus* Distant, *Cosmopsaltria* Stål, *Diceropyga* Stål, *Dilobopyga* Duffels, *Dokuma* Distant, *Dundubia* Amyot & Serville, *Euterpnosia* Matsumura, *Gudaba* Distant, *Haphsa* Distant, *Hyalessa* China, *Inthaxara* Distant, *Kamalata* Distant, *Khimbya* Distant, *Leptopsaltria* Stål, *Lethama* Distant, *Macrosemia* Kato, *Mata* Distant, *Maua* Distant, *Meimuna* Distant, *Moana* J.G. Myers, *Nabalua* Moulton, *Orientopsaltria* Kato, *Platylomia* Stål, *Purana* Distant, *Puranoides* Moulton, *Rhadinopyga* Duffels, *Rustia* Stål, *Semia* Matsumura, *Sinapsaltria* Kato, *Sinosemia* Matsumura, *Taiwanosemia* Matsumura, *Tanna* Distant, *Terpnosia* Distant, *Tosena* Amyot & Serville, *Trengganua* Moulton (*sensu* Metcalf, 1963; Duffels & van der Laan, 1985; Duffels, 1983; Beuk, 2002).

Duffels & van der Laan (1985) list five subtribes: Terpnosiina Kato (=Terpnosiaria *auct.*), Leptopsaltriina Moulton (= Leptopsaltriaria *auct.*), Dundubiina Matsumura (= Dundubiaria *auct.*), Cosmopsaltriina Kato (= Cosmopsaltriaria *auct.*) and Tosenina Amyot & Serville (= Tosenaria *auct.*). However, Lee & Hayashi (2003) recognize four subtribes: Dundubiina, Cosmopsaltriina, Tosenina and Cicadina Latreille, but see Discussion below. Only the subtribe Cosmopsaltriina is relevant to the Australian fauna.

Distribution. Oriental and Australasian regions.

Diagnosis. Timbal covers partly covering timbal cavity; wings hyaline, sometimes with infuscations; basal cell of fore wing more than twice as long as broad; interior ulnar area (?= ulnar area 3) not, or but very slightly, amplified towards the apex; fore wing veins M and CuA very close or contiguous at basal cell; thorax narrowed forwards; lateral margin of pronotum distinctly angulated or toothed; male abdominal sternum thin, male opercula elongate (Atkinson, 1886; Distant, 1905a, 1912; Kato, 1956; Liu, 1978).

Discussion. Atkinson's characterization of this tribe (Atkinson, 1886) was unusually detailed for its time. Distant (1905a) redefined the tribe, essentially by omitting characters included by Atkinson. There has been no subsequent overview of the tribe.

Lee & Hayashi (2003: 170) concluded that the Cicadini and Dundubiini should be amalgamated but gave no reasons for this conclusion. They placed the Cicadini as a subtribe of Dundubiini and included in their new subtribe Cicadina the subtribes Terpnosiina and Leptopsaltriina, but again without stating reasons. Thus, they recognize four subtribes within the Dundubiini; Cicadina and the previously recognized subtribes Dundubiina, Cosmopsaltriina and Tosenina. However, by doing this they inadvertently placed the older of the two family-group names in synonymy. Family group names based on *Cicada* date from Latreille, 1802, those on *Dundubia* from Atkinson, 1886 (see discussion under Cicadidae/Cicadinae p. 387). Thus, Lee & Hayashi's tribal concept should be called Cicadini, not Dundubiini.

Dundubiini, subtribe Cosmopsaltriina Kato, 1932

Type genus. *Cosmopsaltria* Stål (type species: *Cicada doryca* Boisduval).

Included genera. *Aceropyga* Duffels, *Brachylobopyga* Duffels, *Cosmopsaltria* Stål, *Diceropyga* Stål, *Dilobopyga* Duffels, *Meimuna* Distant, *Moana* J.G. Myers, *Rhadinopyga* Duffels (*sensu* Duffels, 1983, 1993; Beuk, 2002).

Distribution. Southeast Asia (excluding continental SE Asia) and Australasia.

Diagnosis. Long lateral processes to the male pygofer (Duffels, 1993, 1997).

Discussion. Duffels (1983, 1986, 1993, 1997) redefined this subtribe and showed that the subfamily Moaninae, represented by the single genus *Moana*, forms part of this subtribe (Duffels, 1993). Duffels & Turner (2002) have provided a phylogeny for the Cosmopsaltriina. Beuk (2002) also provided a phylogeny for the Cosmopsaltriina as well as the Dundubiina and their relationships.

Gymnotympanini Boulard, 1979

Type genus. *Gymnotympana* Stål (type species: *Cicada strepitans* Stål).

Discussion. The tribe Gymnotympanini was separated from the Chlorocystini by Boulard (1979a) on the grounds that the species possessed only 8 apical cells in the fore wing. However, Boer (1995b, 1997) has since concluded from an extensive analysis of Gymnotympanini and Chlorocystini that Gymnotympanini does not warrant separate status. Thus, Gymnotympanini falls as a junior synonym of Chlorocystini, *q.v.*, p. 390.

Hemidictyini Distant, 1905

Type genus. *Hemidictya* Burmeister (type species: *H. frondosa* Burmeister).

Included genera. *Hemidictya* Burmeister, *Hovana* Distant (*sensu* Boer, 1997).

Discussion. A tribe no longer including Australian genera. Boer (1995b, 1997) showed that the two Australian genera believed to belong to this tribe, viz. *Cystopsaltria* and *Cystosoma*, clearly do not form a monophyletic group with *Hemidictya*. The tribe thus falls beyond the scope of this study and is not considered further. See also Chlorocystini, p. 390.

Lyristini Gomez-Menor, 1957

Type genus. *Lyristes* Horváth, 1926 (type species: *Cicada plebeja* Scopoli).

Discussion. No longer a recognized tribe. Boulard (1988a,b, 1998) convincingly argued that *Lyristes* was not an objective junior synonym of *Tibicen* because they did not share *Cicada plebeja* Scopoli as their type species as was widely proclaimed. The type species of *Tibicen* is *Cicada haematodes* Scopoli, a very different species belonging to a different subfamily. Thus, the Tibicenini take on an entirely new meaning and its former concept necessarily changes name to the Lyristini Gomez-Menor, a family-group name already available for the group[1]. See also comments under Tibicenini, p. 393.

However, Boulard (1979b) and Hayashi (1987: 124) had already abandoned the Lyristini by including them as a part of the Cryptotympanini, a concept again maintained by Boulard (1996a,b). Chou *et al*. (1997) also followed this broader tribal concept but have erroneously retained the name Lyristini. See also Cryptotympanini, p. 390.

Parnisini Distant, 1905

Type genus. *Parnisa* Stål (type species: *Cicada propones* Walker).

Included genera. *Abagazara* Distant, *Acyroneura* Torres, *Adeniana* Distant, *Arcystasia* Distant, *Bijaurana* Distant, *Calopsaltria* Stål, *Calyria* Stål, *Chrysocicada* Boulard, *Derotettix* Berg, *Diemeniana* Distant, *Gudanga* Distant, *Henicotettix* Stål, *Jassopsaltria* Ashton, *Lycurgus* China, *Malgotilia* Boulard, *Mapondera* Distant, *Masupha* Distant, *Parnisa* Stål, *Prunasis* Stål, *Psilotympana* Stål, *Quintilia* Stål, *Taipinga* Distant, *Zouga* Distant (*sensu* Metcalf, 1963; Duffels & van der Laan, 1985; Chou *et al*., 1997).

Distribution. All zoogeographic regions; in the Palaearctic confined to the extreme east.

Diagnosis. Timbal covers absent; eyes not projecting (or, at least, not distinctly so) beyond the anterior angles of the pronotum; wings hyaline; pronotum more or less subquadrate; abdomen usually short, not longer than the space between apex of head and base of cruciform elevation (Distant, 1905f, 1906a; Liu, 1978).

Discussion. As a tribe this group has received little attention. There has been no revision since Distant first erected the tribe (Distant, 1905f).

Platypleurini Schmidt, 1918

Type genus. *Platypleura* Amyot & Serville (type species *Cicada stridula* L.).

Included genera. *Afzeliada* Boulard, *Attenuella* Boulard, *Brevisiana* Boulard, *Esada* Boulard, *Hainanosemia* Kato, *Ioba* Distant, *Kalabita* Moulton, *Koma* Distant, *Kongota* Distant, *Muansa* Distant, *Munza* Distant, *Oxypleura* Amyot & Serville, *Platypleura* Amyot & Serville, *Pycna* Amyot & Serville, *Sadaka* Distant, *Severiana* Boulard, *Soudaniella* Boulard, *Strumosella* Boulard, *Suisha* Kato, *Ugada* Distant, *Umjaba* Distant, *Yanga* Distant (*sensu* Metcalf, 1963; Duffels & van der Laan, 1985; Chou *et al*., 1997).

There are two subtribes: Platypleurina (= Platypleuraria *auct.*) (see below) and Hainanosemiina (= Hainanosemiaria *auct.*); only *Hainanosemia, Kalabita* and *Ugada* are included in the latter. More recently Boulard (1998: 117) appears to have incorporated the Cryptotympanini within the Platypleurini by placing the type species of *Cryptotympana, C. atrata* (F.), in the subtribe Cryptotympanina of the tribe Platypleurini, but gives no explanation for doing so. This, of course, would substantially broaden the concept of the Platypleurini.

Distribution. Afro-tropical and Oriental regions. Within Australian territories only known from Christmas Island, Indian Ocean.

Diagnosis. Timbal covers entirely or almost entirely covering timbal cavity; width of head very close to that of mesonotum; eyes generally not too protruding; antennae with 8 segments; pronotal lateral margin dilated; fore wing hyaline, translucent or distinctly maculate, with 8 apical cells; precostal area of fore wing more or less dilated; hind

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[1] Boulard (1988a, 1998) not only argued the case for the change to Lyristini but he also recognized the subfamily name Lyristinae as a replacement for Platypleurinae (= Tibiceninae) (*sensu* Boulard, 1976a). Later, (Boulard, 1996a), he corrected Lyristinae to Platypleurinae.

wings with 6 or sometimes 5 apical cells; cruciform elevation normal in shape, body often massive (Kato, 1956, 1961; Boulard, 1973a, 1996a).

Discussion. The tribe has never been evaluated as a whole and the current diagnosis remains that of Kato (1956, 1961).

Prasiini Matsumura, 1917

Type genus. *Prasia* Stål (type species *P. faticina* Stål).

Included genera. *Arfaka* Distant, *Iruana* Distant, *Jacatra* Distant, *Lacetas* Karsch, *Lembeja* Distant, *Prasia* Stål, *Sapantanga* Distant (*sensu* Metcalf, 1963; Duffels & van der Laan, 1985).

Distribution. Oriental, Australian and Afro-tropical regions; the inclusion of the latter requires confirmation.

Diagnosis. Timbal covers absent; a very narrow vertex, with the ocelli close together; a large obconical and triangularly protruding postclypeus; a very narrow hyaline border along the hind margin of the hind wing; well-developed and posteriorly projecting protuberances on the lateral lobes of the male pygofer (based on the Oriental/Australian Prasiini, Boer, 1995b).

Discussion. Little is known of the African Prasiini and their inclusion in this tribe awaits confirmation. The Oriental and Australian Prasiini have been reviewed by Jong (1982, 1985, 1986, 1987); Jong & Duffels (1981) and Boer (1995b, 1997).

Taphurini Distant, 1905

Type genus. *Taphura* Distant (type species *T. misella* Stål).

Included genera. *Abricta* Stål, *Aleeta* Moulds, *Abroma* Stål, *Auta* Distant, *Burbunga* Distant, *Dorachosa* Distant, *Dulderana* Distant, *Elachysoma* Torres, *Hea* Distant, *Hylora* Boulard, *Imbabura* Distant, *Kanakia* Distant, *Lemuriana* Distant, *Ligymolpa* Karsch, *Malagasia* Distant, *Malgachialna* Boulard, *Marteena* Moulds, *Monomatapa*, Distant, *Musimoia* China, *Nelcyndana* Distant, *Neomuda* Distant, *Nosola* Stål, *Oudeboschia* Distant, *Panka* Distant, *Parnkalla* Distant, *Prosotettix* Jacobi, *Psallodia* Uhler, *Selymbria* Stål, *Taphura* Stål, *Trismarcha* Karsch, *Tryella* Moulds, *Ueana* Distant, *Viettealna* Boulard (*sensu* Metcalf, 1963; Duffels & van der Laan, 1985; Chou *et al.*, 1997).

Distribution. All faunal regions except the Nearctic and poorly represented in the Palaearctic.

Diagnosis. Timbal covers absent; lateral margins of pronotum not developed or dilated; fore wings hyaline; head normal in size and shape; eyes adjacent to anterolateral corner of pronotum; pronotum subquadrate, not distinctly narrowed anteriorly; abdomen about as long as space between apex of head and base of cruciform elevation (except in *Malagasia* and *Kanakia*); a more or less distinct posterior metasternal process visible in males between or at the base of the opercula (Kato, 1956; Distant, 1905e, 1906a).

Discussion. There has never been a review of the Taphurini as a whole since Distant erected the tribe in 1905. Its definition and composition have remained more or less unchanged.

Thophini Distant, 1904

Type genus. *Thopha* Amyot & Serville (type species *Tettigonia saccata* F.).

Included genera. *Arunta* Distant, *Thopha* Amyot & Serville (*sensu* Metcalf, 1963; Duffels & van der Laan, 1985; Moulds, 2001).

Distribution. Australia.

Diagnosis. Timbal covers entirely concealing timbals, strongly developed and sac-like, extending to about half abdominal length; opercula small, not reaching base of metasternum; fore and hind wings hyaline; lateral margin of pronotum dilated (Distant, 1904a, 1912; Kato, 1956; Moulds, 2001).

Discussion. The two genera of this tribe are grouped primarily on the basis of their remarkably swollen timbal covers. Duffels & van der Laan (1985) also included *Arenopsaltria* in Thophini but Moulds (1990) followed Metcalf (1963) by placing it in the Cyclochilini. Moulds (2001) redefined the Thophini.

Tibicenini Van Duzee, 1916

Type genus. *Tibicen* Latreille, 1825 (type species *Cicada plebeja* Scopoli, *non*. L.).

Discussion. Now considered a junior synonym of Cryptotympanini, *q.v.* (Boulard, 1998, 2001).

The current usage of the generic name *Tibicen* and its derived family-group names is erroneous. Boulard (1988a,b, 1998, 2001) convincingly argued that *Lyristes* was not an objective junior synonym of *Tibicen* because they did not share *Cicada plebeja* Scopoli as their type species as was widely proclaimed (e.g., China, 1964). The type species of *Tibicen* is *Cicada haematodes* Scopoli, a very different species indeed (which also happens to be the type species of *Tibicina*). Thus, the Tibicenini take on an entirely new meaning and its former concept necessarily changes name to the Lyristini Gomez-Menor, a family-group name already available for the taxon.

Boulard's arguments for this change in type species (Boulard, 1998, 2001) are rather long and complex. I summarize the salient points as follows:

(*a*) There are two species called *Cicada plebeja*; *C. plebeja* Scopoli, 1763 and *C. plebeja* Linnaeus, 1767, which introduces ambiguity when the author is omitted.

(*b*) *Tibicen* does not date from Latreille (1825) as often stated but from Latreille (1829) because the latter lists the first unambiguously included species [Art. 67.2.2].

(*c*) The type species of *Tibicen* is not *Cicada plebeja* Scopoli as generally accepted, but one of the taxa listed by Latreille (1829), i.e. *C. haematodes* Scopoli (= *Tettigonia sanguinea*), which was designated as the type species by Amyot & Serville (1843) as first revisors.

(*d*) Horváth (1926) proposed the generic name *Lyristes*, with type species *Cicada plebeja* Scopoli, by original designation.

This correction to the type species for *Tibicen* has far-reaching consequences at family/subfamily rank (see "Tibiceninae", p. 389). It also means that species traditionally placed in *Tibicen* (e.g., those species listed by Duffels & van der Laan, 1985) must be transferred to *Lyristes.* The ICZN would need to fix the type species of *Tibicen* as *Cicada plebeja* Scopoli if this scenario was to be avoided.

See also Lyristini (p. 392) and Cryptotympanini (p. 390).

Cicadoidea phylogeny

While there has been considerable interest in past years concerning phylogenetic relationships between the Cicadoidea and allied superfamilies within the Hemiptera (e.g., Blocker, 1996; Hamilton, 1981, 1996; Schaefer, 1988, Sorensen *et al.*, 1995), little attempt has been made to resolve relationships within the Cicadoidea.

The substantiation of monophyletic groups at family and subfamily rank have relied largely upon structures associated with sound production and reception, viz. the absence or presence of timbals, development of the timbal covers, the development of the tympana and the presence or absence of accessory stridulatory mechanisms. Only features associated with the genus *Tettigarcta* have traditionally supplemented this list (cf. J.G. Myers, 1929; Evans, 1941; Moulds, 1990).

Previously Singh-Pruthi (1925: 195) had examined male genitalia and suggested some aedeagal characters for subfamily and tribal relationships but his conclusions were ambiguous and have not been adopted by subsequent authors. Hayashi (1984) added to the above the development of the metanotum and a cursory inference to male genitalic structure. Recently Chou *et al.* (1997) used further characters in their assessment of family/subfamily relationships, incorporating not only characters relating to sound production and those associated with Tettigarctidae, but also abdominal size, size of pronotal margin, head/eye size and size of male subgenital plate (more correctly termed sternite VIII) and "efficiency of song".

Substantiation of monophyletic groups at tribal rank has relied on a far wider range of characters. Prominent amongst these are the width of the head, development of the pronotal margin, wing venation and maculation, development of the opercula and abdominal shape (cf. Distant, 1904a,b, 1905a–g; Kato, 1956). More recently characters relating to male genital structures have been used (cf. Boulard, 1979b; Duffels, 1993; Boer, 1995b), characters that are much more specific than those genital characters proposed by Singh-Pruthi (1925). Boulard (1965, 1973a) studied female genital structures and identified characters of potential systematic value, but found only one supporting family group rankings.

The adoption of the above characters to family group systematics requires some specific comment as follows.

The family-group classifications established by Boulard, Hayashi, Kato and others, which remain the basis for classification today, are essentially hierarchical in nature, and there has been little emphasis on establishing relationships. Only Kato (1956) and Chou *et al.* (1997) attempted to elucidate phylogenetic relationships at family-group level.

Kato's phylogeny was derived from intuitive decisions drawn from his extensive knowledge of the world fauna and justification for nodes was far from complete. His phylogeny did, however, incorporate many of the then recognized tribes, many of which are still used today. Kato's phylogeny remains the only phylogeny showing sister relationships at tribal level.

Chou *et al.* attempted a cladistic analysis of family and subfamily relationships, employing modern Hennigian methodology. Their result, however, is limited by taking existing hierarchical groupings and employing apomorphies believed to support those groupings and they used the Tettigarctidae as their outgroup. Thus, they resolve relationships only (excluding Tettigarctidae), and do not test the monophyly of the groupings themselves.

The family/subfamily phylogenies of Kato and Chou *et al.* are virtually identical (taking into account that the Plautillinae and Ydiellinae postdate Kato and consequently are omitted from his tree). This is not surprising because both were applying essentially the same set of "traditional" characters, those associated with the sound producing and receiving mechanisms. Kato remained undecided only on the placement of the Platypediidae or Tettigarctidae as the sister group to all other cicadas, although he suggested that the Tettigarctidae is the more likely.

Additional phylogenetic studies of tribal groupings (e.g., Duffels, 1977, 1983, 1988, 1993; Boer, 1995b, 1997; Duffels & Turner, 2002; Beuk, 2002) have resolved relationships within the tribes they studied. Although a large part of these studies falls beyond the scope of this work some significant results do relate to matters of family-group phylogeny and the phylogeny of genera occurring in Australia, notably the following.

Studies by Duffels (1983, 1993) and Duffels & Turner (2002) of the subtribe Cosmopsaltriina have shown that *Moana expansa*, then representing the family Moaninae, actually belongs to this subtribe. Boer's work on the Chlorocystini has shown that there is no justification for retaining Gymnotympanini as a separate tribe (Boer, 1995b) because the genera comprising Gymnotympanini fall amongst the genera of the Chlorocystini. Further, Boer (1995b, 1997) resolved relationships between the Australian genera of the Chlorocystini while Duffels (1993, 1997), Duffels & Turner (2002) and Beuk (2002) resolved relationships within Cosmopsaltriina which includes the genus *Diceropyga* which ranges to northern Australia. Boer (1995b) also identified the sister group relationships for the Chlorocystini. He concluded that the Prasiini are the most likely sister group, a conclusion similar to that reached by Kato (1956).

PHYLOGENETIC ANALYSIS

Cladistic parsimony is used here to test the monophyly of currently accepted cicada family and subfamily groupings for the first time. Tribal groupings relevant to the Australian cicada fauna, or that are likely to be relevant, are also tested. A complete analysis incorporating representatives of all known cicada genera falls beyond the scope of this work. However, the inclusion of type genera of all current and past families and subfamilies and of representatives of all Australian tribes (including non-Australian type genera) as well as all Australian genera provides a framework for solving such a problem. Thus, I analyse relationships among all Australian genera plus representative species of key genera (usually the type genus) from all families and subfamilies recognized by previous workers (e.g., Distant, 1906b; Kato, 1954, 1956; Boulard, 1973b, 1976a,b; Hayashi, 1984; Duffels, 1993; Moulds, 1990) and all tribes believed to relate to the Australian fauna. Based on the results of this analysis current concepts for the family classification of the Cicadoidea are challenged.

While the long-held concept that the sound organs and allied structures alone can unambiguously reflect phylogenetic relationships may be true, (e.g., Distant, 1906b; Boulard, 1976a, 1986b), all morphological characters considered to reflect phylogeny should be considered if we are to have confidence in resulting trees. I have identified 117 such characters (representing 290 states) from both external and internal anatomy.

Taxon representation: groundplan or exemplar?

When undertaking a cladistic analysis to reconstruct phylogeny of higher taxa (genus rank or above) it is inevitably impractical to code all species as separate terminals. Analyses can proceed in one of two ways: (1) code groundplan character states intuitively deduced from examining a range of member species, or (2) code character states from one or more real species as representatives of the group. The former is known as the groundplan method, the latter the exemplar method.

Both methods give identical results when characters are identical in all members of the terminal species. However, Yeates (1995) shows that this may not be so when character states differ between members of the group. While there is clearly a place for both methods, Yeates argues that the advantages of the exemplar approach outweigh those of the groundplan approach. When a terminal group has multiple character states amongst its members then the character state(s) of the internal node representing the hypothetical common ancestor of the group depends on the states present on both branches leading from the node, and that if either of these branches divide again and the subbranches display multiple states of a character, then the distribution of all states in all subbranches must be taken into account when reconstructing the more basal node. Exemplar methodology is potentially better at addressing this situation by allowing characterization of exemplars rather than an inflexible groundplan characterization which may differ from the characterization of taxa in the group. Where species sister relationships are unknown Yeates suggests using multiple exemplars whenever multiple character states occur. For these reasons I use exemplars as representatives of genera, tribes, subfamilies and families in the analyses detailed below.

Representation of genera

The following species were chosen as representatives of all genera currently recognized as occurring in Australia, including a number of described species believed to represent new genera. Some additional species believed to be wrongly placed in available genera are also included. For the most part, the type species of described genera, including non-Australian species (those marked by an asterisk, *) were selected as representatives. Multiple representatives of genera were avoided except for those that include species with alternative character states or to provide a second representative for a clade, so as to minimize computer logistic problems associated with large cladistic data sets.

Abricta borealis (Goding & Froggatt)
Abricta occidentalis (Goding & Froggatt)
* *Aleeta curvicosta* (Germar)
* *Anapsaltoda pulchra* (Ashton)
* *Arenopsaltria fullo* (Walker)
* *Arunta perulata* (Guerin-Meneville)
* *Birrima castanea* (Goding & Froggatt)
* *Burbunga gilmorei* (Distant)
Burbunga albofasciata Distant
* *Chlorocysta vitripennis* (Westwood)
* *Chrysocicada franceaustralae* Boulard
Cicadetta celis (Moulds)
Cicadetta forresti (Distant)
Cicadetta graminis (Goding & Froggatt)
Cicadetta melete (Walker)
Cicadetta minima (Goding & Froggatt)
* *Cicadetta montana* (Scopoli) [non-Australian]
* *Cyclochila australasiae* (Donovan)
Cyclochila virens Distant
* *Cystopsaltria immaculata* Goding & Froggatt
* *Cystosoma saundersii* Westwood
Diceropyga subapicalis (Walker)
* *Diemeniana frenchi* (Distant)
* *Froggattoides typicus* Distant
* *Glaucopsaltria viridis* Goding & Froggatt
* *Gudanga boulayi* Distant
* *Guineapsaltria flava* (Goding & Froggatt)
* *Gymnotympana strepitans* (Stål) [non-Australian]
Gymnotympana varicolor (Distant)
* *Henicopsaltria eydouxii* (Guerin-Meneville)
Henicopsaltria rufivelum Moulds
* *Illyria burkei* (Goding & Froggatt)
* *Jassopsaltria rufifacies* Ashton
Jassopsaltria sp. A
Lembeja vitticollis (Ashton)
* *Kikihia subalpina* (Hudson) [non-Australian]
* *Kobonga umbrimargo* (Walker)
* *Macrotristria angularis* (Germar)
Macrotristria hillieri (Distant)
Macrotristria intersecta (Walker)
* *Marteena rubricincta* (Goding & Froggatt)
* *Neopsaltoda crassa* Distant
Notopsalta atrata (Goding & Froggatt)
* *Owra insignis* Ashton
Oxypleura calypso (Kirby)
* *Parnkalla muelleri* (Distant)
Pauropsalta basalis (Goding & Froggatt)
Pauropsalta circumdata (Walker)
Pauropsalta encaustica (Germar)
Pauropsalta eyrei (Distant)
* *Pauropsalta mneme* (Walker)
Pauropsalta sp. M
Pauropsalta nodicosta (Goding & Froggatt)
* *Psaltoda moerens* (Germar)
Quintilia infans (Walker)
* *Tamasa tristigma* (Germar)
* *Tettigarcta crinita* Distant
Thaumastopsaltria globosa (Distant)
* *Thopha saccata* (Fabricius)
* *Tryella ochra* Moulds
Urabunana marshalli (Distant)
* *Urabunana sericeivitta* Walker
* *Venustria superba* Goding & Froggatt

Representation of tribes and higher taxa

The following non-Australian species have been included, in addition to the list above, as part of a broader analysis of relationships. They are key representatives of tribal groupings (usually the type species) that are believed to have Australian affinities, or of family and subfamily groupings that at any time have been recognized in Cicadoidea classification. It was possible to obtain representatives of all family and subfamily groupings previously proposed except for the Ydiellinae Boulard. This omission is considered tenable as Boulard (1993) now implies that it should rank only at subtribal level. The 20 or so tribal groupings excluded from representation are distinctive South American tribes or non-Australian tribes from Asia and Africa. They have been excluded because they fall beyond the scope of this study and to minimize computer logistic problems associated with large cladistic data sets.

Cicada orni Linnaeus
Cicadetta montana (Scopoli)
Cosmopsaltria doryca (Boisduval)
Cryptotympana facialis (Walker)
Dundubia vaginata (Fabricius)
Gymnotympana strepitans (Stål)
Lyristes (= Tibicen) plebejus (Scopoli)
Magicicada septendecim (Linnaeus)
Odopoea dilatata (Fabricius)
Parnisa designata (Walker)
Platypedia putnami (Uhler)
Platypleura stridula Linnaeus
Plautilla venedictoffae Boulard
Prasia faticina Stål
Taphura misella (Stål)
Tettigades ulnaria Distant
Tibicina haematodes (Scopoli)
Zammara intricata Walker

A list of the family-group taxa represented and their representative species is as follows. Type genera of family-group names are marked by an asterisk (*). Names of species not occurring in Australia are in bold face.

CHLOROCYSTINI (_sensu_ Duffels & van der Laan, 1985; Boer, 1995b): *_Chlorocysta vitripennis, Cystopsaltria immaculata, Cystosoma saundersii, Glaucopsaltria viridis, Guineapsaltria flava, Gymnotympana varicolor, Gymnotympana strepitans, Owra insignis, Thaumastopsaltria globosa, Venustria superba._

CICADETTINI (_sensu_ Duffels & van der Laan, 1985): _Cicadetta celis, Cicadetta forresti, Cicadetta melete, Cicadetta minima,_ *__Cicadetta montana__, _Birrima castanea, Froggattoides typicus,_ **_Kikihia subalpina_**, _Kobonga umbrimargo, Notopsalta atrata, Pauropsalta basalis, Pauropsalta eyrei, Pauropsalta_ sp. M, _Pauropsalta mneme, Pauropsalta nodicosta, Urabunana marshalli, Urabunana sericeivitta._

CICADIDAE/CICADINAE (_sensu_ Hayashi, 1984; Moulds, 1990): _Anapsaltoda pulchra, Arenopsaltria fullo, Arunta perulata, Burbunga gilmorei,_ *__Cicada orni, Cosmopsaltria doryca, Cryptotympana facialis__, _Cyclochila australasiae, Cyclochila virens, Diceropyga subapicalis,_ **_Dundubia vaginata_**, _Henicopsaltria eydouxii, Illyria burkei,_ **_Lyristes plebejus_** _(= Tibicen plebejus), Macrotristria angularis, Macrotristria hillieri, Neopsaltoda crassa, Oxypleura calypso, Psaltoda moerens, Tamasa tristigma, Thopha saccata._

CICADINAE (_sensu_ Boulard, 1976a, 1996a): *__Cicada orni, Cosmopsaltria doryca__, _Cyclochila australasiae, Cyclochila virens, Diceropyga subapicalis,_ **_Dundubia vaginata_**, _Illyria burkei, Tamasa tristigma._

CICADINI (_sensu_ Duffels & van der Laan, 1985): *__Cicada orni__, _Illyria burkei, Tamasa tristigma._

COSMOPSALTRIINA (_sensu_ Duffels, 1983; Duffels & Turner, 2002; Beuk, 2002): *__Cosmopsaltria doryca__, _Diceropyga subapicalis._

CRYPTOTYMPANINA (_sensu_ Duffels, 1983, 1993): *__Cryptotympana facialis__.

CRYPTOTYMPANINI (_sensu_ Hayashi, 1987; Boulard, 1988a,b, 1996a): _Anapsaltoda pulchra,_ *__Cryptotympana facialis__, _Macrotristria angularis, Macrotristria hillieri, Psaltoda moerens, Neopsaltoda crassa, Lyristes plebejus (= Tibicen plebejus)._

CYCLOCHILINI (_sensu_ Duffels & van der Laan, 1985): _Anapsaltoda pulchra, Arenopsaltria fullo,_ *_Cyclochila australasiae, Cyclochila virens, Henicopsaltria eydouxii, Neopsaltoda crassa, Psaltoda moerens._

DUNDUBIINA (_sensu_ Duffels & van der Laan, 1985): *__Dundubia vaginata__.

DUNDUBIINI (_sensu_ Duffels & van der Laan, 1985; Beuk, 2002): _Diceropyga subapicalis,_ *__Dundubia vaginata, Cosmopsaltria doryca__.

GYMNOTYMPANINI (_sensu_ Boulard, 1979a, 1993): *__Gymnotympana strepitans__, *_Gymnotympana varicolor._

PARNISINI (_sensu_ Duffels & van der Laan, 1985): _Diemeniana frenchi, Gudanga boulayi, Jassopsaltria rufifacies, Jassopsaltria_ sp. A, *__Parnisa designata__, _Quintilia infans._

PLATYPEDIIDAE/PLATYPEDIINAE (_sensu_ Boulard, 1973b, 1976b): *__Platypedia putnami__.

PLATYPLEURINA (_sensu_ Duffels & van der Laan, 1985): _Oxypleura calypso,_ *__Platypleura stridula__.

PLATYPLEURINAE (=TIBICENINAE) (_sensu_ Boulard, 1976a): _Anapsaltoda pulchra, Arunta perulata,_ **_Cosmopsaltria doryca, Cryptotympana facialis_**, _Diceropyga subapicalis,_ **_Dundubia vaginata_**, _Henicopsaltria eydouxii,_ **_Lyristes plebejus_** _(=Tibicen plebejus), Macrotristria angularis, Macrotristria hillieri, Neopsaltoda crassa, Oxypleura calypso,_ **_Platypleura stridula_**, _Psaltoda moerens, Thopha saccata._

PLATYPLEURINI (_sensu_ Duffels & van der Laan, 1985): _Oxypleura calypso,_ *__Platypleura stridula__.

PLAUTILLIDAE/PLAUTILLINAE (_sensu_ Boulard, 1976b): *__Plautilla venedictoffae__.

PRASIINI (_sensu_ Duffels & van der Laan, 1985): _Lembeja vitticollis,_ *__Prasia faticina__.

TAPHURINI (_sensu_ Duffels & van der Laan, 1985; Moulds, 1990; Boulard, 1993): _Abricta borealis, Abricta occidentalis, Aleeta curvicosta, Burbunga albofasciata, Burbunga gilmorei, Marteena rubricincta, Parnkalla muelleri,_ *__Taphura misella__.

TETTIGADIDAE/TETTIGADINAE (*sensu* Metcalf, 1963; Duffels & van der Laan, 1985): ***Tettigades ulnaria*.**

TETTIGARCTIDAE (*sensu* Boulard, 1976a; Hayashi, 1984; Moulds, 1990): **Tettigarcta crinita*.

THOPHINI (*sensu* Duffels & van der Laan, 1985; Moulds, 1990, 2001): *Arunta perulata, *Thopha saccata.*

TIBICENINAE: see PLATYPLEURINAE

TIBICENINI: see CRYPTOTYMPANINI

TIBICINIDAE/TIBICININAE (*sensu* Hayashi, 1984; Moulds, 1990; Boulard, 1993): *Abricta borealis, Abricta occidentalis, Aleeta curvicosta, Birrima castanea, Burbunga gilmorei, Chlorocysta vitripennis, Chrysocicada franceaustralae, Cicadetta celis, Cicadetta forresti, Cicadetta graminis, Cicadetta melete, Cicadetta minima,* ***Cicadetta montana****, Cystopsaltria immaculata, Cystosoma saundersii, Diemeniana frenchi, Froggattoides typicus, Glaucopsaltria viridis, Gudanga boulayi, Guineapsaltria flava, Gymnotympana strepitans, Gymnotympana varicolor, Jassopsaltria rufifacies, Jassopsaltria* sp. A, *Kikihia convicta,* ***Kikihia subalpina****, Kobonga umbrimargo, Lembeja vitticollis,* ***Magicicada septendecim****, Marteena rubricincta, Notopsalta atrata, Owra insignis, Parnkalla muelleri, Pauropsalta basalis, Pauropsalta eyrei, Pauropsalta* sp. M, *Pauropsalta mneme, Pauropsalta nodicosta, Thaumastopsaltria glauca,* ****Tibicina haematodes****, Tryella ochra, Urabunana marshalli, Urabunana sericeivitta, Venustria superba.*

TIBICININI (*sensu* Metcalf, 1963; Duffels & van der Laan, 1985): ***Magicicada septendecim, *Tibicina haematodes*.**

ZAMMARINI (*sensu* Metcalf, 1963; Duffels & van der Laan, 1985): ***Odopoea dilatata, Zammara intricata*.**

Choice of outgroup

Within the Cicadoidea (i.e. the cicadas), the Tettigarctidae are widely considered to have several synapomorphic character states placing them as the sister group of all other cicadas (hereafter referred to as the family Cicadidae, *sensu* Moulds, 1990) (Evans, 1956, 1963; Moulds, 1990; Moulds & Carver, 1991). In this regard the Tettigarctidae is an obvious outgroup choice for a cladistic analysis of the Cicadidae. The Tettigarctidae contain just two extant species, *Tettigarcta crinita* and *T. tomentosa* [both very similar and both Australian endemics (Moulds, 1990)], and several fossil genera from the Northern Hemisphere (Nel, 1996). *Tettigarcta crinita* together with *T. tomentosa* have been chosen as the outgroup for the Cicadidae.

However, for an analysis of the Cicadoidea as a whole, the Tettigarctidae become part of the ingroup and a new outgroup is required, ideally one from the sister group of the Cicadoidea so as to maximize chances for finding homologous characters. The Cicadoidea form part of a broader natural grouping, the infraorder Cicadomorpha comprising the superfamilies Cicadoidea, Cercopoidea and Membracoidea (= Cicadelloidea) (Evans, 1946, 1951; Hamilton 1981, 1996; Sweet, 1996; Blocker, 1996). Within this grouping Evans (1977) proposed that Cicadoidea and Cercopoidea were sister groups based on morphological evidence. Hamilton (1981) concurs with this arrangement using evidence from head morphology. Also Schaefer (1988) reaches the same conclusion following ecological evidence. Both Blocker (1996) and Shcherbakov (1996) also agree that Cicadoidea and Cercopoidea are sister groups primarily on the basis of fossil evidence. On the other hand, Hamilton (1996) provides persuasive arguments for placing the Membracoidea, rather than the Cercopoidea, as the sister group of Cicadoidea based on fossil evidence.

These differences of opinion make little difference to outgroup selection. The Cercopoidea and Membracoidea are far more similar to each other than they are to the Cicadoidea (see characterizations of Kramer, 1950). Because of the available evidence favouring the Cercopoidea as the closest sister group of Cicadoidea, a selection has been made from this superfamily; a large and somewhat cicada-like *Megastethodon* sp., family Cercopidae, has been chosen as the outgroup taxon.

Tree searching

Data were analysed initially using the heuristic search parsimony algorithms implemented with PAUP* version 4.0b2 (TBR + RAS–10, MULPARS) (Swofford, 1998). When an island of tree problem (Maddison, 1991) became evident the search was expanded to cover more random addition sequence starting trees. Searches were continued until no new islands were found.

Cladograms (Figs. 59–62) were prepared using CLADOS version 1.2 (Nixon, 1992) with DELTRAN optimization from trees generated by HENNIG86, version 1.5 (Farris, 1989a). Character numbers on these trees were adjusted to begin at “1”, rather than the “zero” default.

Characters

Data for 117 characters (representing 290 states) considered meaningful at either family or species group level were derived from either adult morphology, including internal reproductive systems (112 characters), or from nymphal morphology (5 characters). Species group characters were limited to those characters necessary for defining genera when more than one species for a genus was included in the analysis. Morphometric characters were largely avoided because of their substantially subjective nature and the difficulty of measuring continuous variables one against another (e.g., body size and wing length); more importantly they largely apply at species-group level rather than at family-group level.

All multistate characters were treated as unordered (= non-additive) because alternative arrangements were considered equally plausible (e.g., characters 1, 7, 38 and 58 for example). No *a priori* determination of character polarities was made. Polarities were determined as a consequence of using cladistic parsimony principles by rooting cladograms with an outgroup (Nixon & Carpenter, 1993). Neither character weighting or successive weighting was employed. Missing and inapplicable data are scored as “?”. The matrix of taxa and assigned states is given in Table 1. Refer to Figs. 1–30 for explanations of morphological terms. Additional figures and comments on selected characters are included with the character descriptions.

Table 1. Character matrix of the 81 taxa used in the parsimony analysis. Missing data and character states not relevant to a taxon are scored as "?".

	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000001	1111111111	1111111
	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	8888888889	9999999990	0000000001	1111111
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567
Cercopidae	?0?00???00	??0???????	0????0??0?	0???????0?	?0?????0??	0?????0?0?	????????0?	???????000	?0??000100	0000000000	0000000000	0?00000
Abricta borealis	0010000100	001000?000	1100100000	0101001100	0000???010	0110??1011	1020201100	2101011000	0000??1011	1??1111111	1111110000	0?00000
Abricta occidentalis	0000000000	001020?000	0100100000	0101000400	0000???100	0110??1011	1030201201	1?30?00000	0000??1011	1??1111111	1111110000	0?00000
Aleeta curvicosta	1000000000	001000?000	0100100000	1101000400	0010???100	0110??2211	1130201201	1?30?00000	0011111011	1111111111	1111110000	0000000
Anapsaltoda pulchra	2000011000	010000?000	0000100000	0001000200	1022030001	010??01001	0?10102400	1?10?00000	0000??1011	1??1111111	1111110000	0?00000
Arenopsaltria fullo	2000000000	010000?000	0001100000	0001000200	1002030001	00????1011	0?10002400	1?10?00000	0000??1011	1??1111111	1111110000	0?00000
Arunta perulata	2000010000	010000?000	0001100000	0001000600	10121?0001	00????1011	0?10001900	1?00?00000	0000121011	1111111111	1111110000	0000000
Burbunga albofasciata	2000000000	000000?000	0001100000	0001000000	0002000001	00????1011	0?10002400	1?40?00000	0000??1011	1?11111111	1111110000	0?00000
Burbunga gilmorei	2000000000	0?0000?000	0001100000	0001000000	0002000001	00????1011	0?10202400	1?40?00000	00001?1011	1?11111111	1111110000	0?00000
Birrima castanea	0010000000	001000?000	0400100000	0101001100	0010???010	0110??1011	1020203600	1?01200100	1000011011	1111111111	1111110000	0000000
Chlorocysta vitripennis	0110000000	0010311111	011?100011	0101000311	0000???100	010??11111	1030201500	1?20?00000	0000121011	1?11111111	1111110000	0?00000
Chrysocicada franceaustralae	0000000000	001000?000	0100100000	0101000400	0010???100	0110??1001	1130201201	1?30?00000	0000??1011	1??1111111	1111110000	0?00000
Cicada orni	1000000000	010000?000	0101100000	0001000000	0102001001	00????1021	0?10002300	1?10?00000	00001?1011	1?11111111	1111110000	0?00000
Cicadetta celis	0010000000	001000?000	0400100000	0101001100	0000???010	0110??1011	1020203600	1?01200100	1000?21011	11?1111111	1111110000	0000000
Cicadetta forresti	0010000000	001000?000	0400100000	0101001800	0000???110	01110?1011	1020201?00	2001100000	0000??1011	1??1111111	1111110000	0?00000
Cicadetta graminis	0010000000	001000?010	0400100001	0101001100	0000???010	0113??1211	1020201700	2001100000	0000??1011	1??1111111	1111110000	0?00000
Cicadetta labeculata	0010000000	001000?000	0400100000	0101001100	0000???010	0110??1011	1020201100	2101011000	0000?21011	1??1111111	1111110000	0?00000
Cicadetta minima	0010000000	001000?010	0400100001	0101001100	0000???010	01130?1211	1020201700	2001100000	0000??1011	1??1111111	1111110000	0?00000
Cicadetta montana	0010000000	001000?000	0300100000	1101001100	00?0???010	0110??1011	1020203600	1?01200000	0000??1011	1??1111111	1111110000	0?00000
Cosmopsaltria doryca	1000000100	010000?000	0101100000	0011000500	1102021002	00????1021	2?11002?00	1?00?00000	0000??1011	1??1111111	1111110000	0?00000
Cryptotympana facialis	2000010000	010000?000	0000100000	0001000200	1002030001	00????1011	0?10002400	1?10?00100	0000??1011	1??1111111	1111110000	0?00000
Cyclochila australasiae	1000022010	010000?000	0001110000	0001020200	?002000001	00????1011	0?10002400	1?10?00000	0000121011	1111111111	1111110000	0000000
Cyclochila virens	1000022010	010000?000	0001110000	0001020200	?002000001	00????1011	0?10002400	1?10?00000	0000121011	1111111111	1111110000	0000000
Cystopsaltria immaculata	0110000000	10105???0?	010?10110?	0101100111	0000???100	010??11111	1030201500	1?20?00000	0000??1011	1??1111111	1111110000	0?00000
Cystosoma saundersii	0110000000	10105???0?	020?10110?	0101100111	0000???100	010??11111	1030201500	1?20?00000	0000111011	1111111111	1111110000	0000000
Diceropyga subapicalis	1000000100	000000?000	0101100000	0011000500	1102021002	00????1021	2?11002?00	1?00?00100	0000??1011	1??1111111	1111110000	0?00000
Diemeniana frenchi	0010000100	001000?000	0100100000	0101000100	0000???010	0110??1011	1020201100	2101011000	0000021011	1111111111	1111110000	0000000
Dundubia vaginata	1000010100	010000?000	0101100000	0011000500	1102021001	00????1021	0?10002300	1?10?00000	0000??1011	1??1111111	1111110000	0?00000
Froggattoides typicus	0000000000	001000?000	0400100000	0111001100	0000???010	00????1011	1020201?00	2101011000	0000??1011	1??1111111	1111110000	0?00000
Glaucopsaltria viridis	0110000000	0010411111	011?100010	0101000311	0000???100	010??11111	1030201500	1?20?00000	0000??1011	1??1111111	1111110000	0?00000
Gudanga boulayi	0000000000	001000?00?	0100100000	0101000100	0000???010	01110?1011	1020201100	1?01010000	0000??1011	1??1111111	1111110000	0?00000
Guineapsaltria flava	0110000000	001000?011	0110100000	0101000311	0000???100	010??11111	1030201500	1?20?00000	00000?1011	1?11111111	1111110000	0?00000
Gymnotympana varicolor	0110000000	001000?011	0110100000	0111000311	0000???100	010??11111	1030201500	1?20?00000	0000??1011	1??1111111	1111110000	0?00000
Gymnotympana strepitans	0110000000	001000?011	0110100000	0111000711	0000???100	010??11111	1030201500	1?20?00000	0000??1011	1??1111111	1111110000	0?00000
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Henicopsaltria rufivelum	2000000000	0?0000?000	0001100000	0001000200	1002030001	010??01001	0?10002400	1?10?00000	0000??1011	1111111111	1111110000	0000000
Illyria burkei	2000000000	010000?000	0001100000	0001000600	0002020002	00????1001	0?10002400	1?10?00000	0100?11011	11?1111111	1111110000	0000000
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Jassopsaltria sp A	1000100000	000000?000	0001100000	0001000000	000200000?	00????1001	0?10002400	1?10?00000	0000??1011	1??1111111	1111110000	0?00000
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	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	8888888889	9999999990	0000000001	1111111
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567
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Macrotristria hillieri	2000000000	000000?000	0001100000	0001000000	0002000002	00????1011	0?10002400	1?40?00000	0000??1011	1?11111111	1111110000	0?00000
Macrotristria intersecta	2000010000	010000?000	0001100000	0001000200	0002020001	00????1011	0?10002400	1?10?00000	0100??1011	1111111111	1111110000	0000000
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Marteena rubricinctus	0010000100	001000?000	1100100000	0101001100	0000???010	0110??1011	1020201100	2101011000	0000??1011	1??1111111	1111110000	0?00000
Notopsalta atrata	0010000000	001000?000	0400100000	0101001100	0000???010	0110??1011	1020201100	2101011000	0000??1011	1??1111111	1111110000	0?00000
Odopoea dilatata	0011003000	000100?000	0201100000	0011100000	0002010001	00????1011	0?10000100	1?00?00000	0000???011	1??1111111	1111110000	0?00000
Owra insignis	0110000000	0010210111	011?101001	0101000?11	0000???100	010??11111	1030201500	1?20?00000	0000??1011	1??1111111	1111110000	0?00000
Oxypleura calypso	2000003000	010000?000	0001100001	0001100200	0002020001	00????1011	0?10002400	1?00?00000	0000??1011	1??1111111	1111110000	0?00000
Parnisa designata	01?0000000	001010?011	0100100001	0101000110	0000???100	010??01111	103020??0?	1??0?00000	0000???011	1??1111111	1111110000	0?00000
Parnkalla muelleri	1000000000	010000?000	0101100000	0001000000	000????001	00????1011	0?10001710	1?00?00000	00000?1011	1?11111111	1111110000	0?00000
Pauropsalta basalis	0010000000	001000?010	0400100001	0101001101	0000???010	0113??1211	1020201700	2001100000	0000??1011	1??1111111	1111110000	0?00000
Pauropsalta circumdata	0010000000	001000?000	0400100000	1101001100	0000???010	11111?1011	1020201700	2001100000	0000??1011	1?11111111	1111110000	0?00000
Pauropsalta encaustica	0010000000	001000?000	0400100001	1101001100	0000???010	11111?1011	1020201700	2001100000	0000?21011	1?11111111	1111110000	0?00000
Pauropsalta eyrei	0010000000	001000?010	0400100000	0101001100	0000???010	01111?1211	1120201700	2001100100	0000021011	1111111111	1111110000	0000000
Pauropsalta sp M	0010000000	001000?010	0400100001	0101001100	0000???010	01111?1211	1120201700	2001100100	00000?1011	1111111111	1111110000	0000000
Pauropsalta mneme	0010000100	001000?000	0400100001	1101001100	0000???010	01110?1011	1020201700	2001100000	0000021011	1?11111111	1111110000	0?00000
Pauropsalta nodicosta	0000000000	001000?020	0400100001	0101001800	0000?????0	0110??1011	1020201100	?101011000	0000??1011	1??1111111	1111110000	0000000
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Prasia faticina	01?0000000	101000?00?	1100101000	0111000100	0000???100	010??01111	1030201100	1??0?00000	0000??1011	1??1111111	1111110000	0?00000
Psaltoda moerens	2000011000	010000?000	010?100000	0001000200	1022030001	010??01001	0?10102400	1?10?00000	0000111011	1111111111	1111110000	0000000
Quintilia infans	00?0000000	001000?000	0100100000	0101001101	0000???010	0110??1011	1020201100	2101011000	0000??1011	1??1111111	1111110000	0?00000
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Tettigarcta crinita	00000?0000	0?0000??0?	0?00010000	000011??00	0000???000	00????0?00	0?0030400?	0?00?00000	?000000011	1110000000	0000001111	1111111
Tettigarcta tomentosa	00000?0000	0?0000??0?	0?00010000	000011??00	0000???000	00????0?00	0?0030400?	0?00?00000	?000000011	1110000000	0000001111	1111111
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Urabunana marshalli	0000000000	001000?010	0400100001	0101001100	0000???010	0110??1011	1120201800	2001300000	0000??1011	1??1111111	1111110000	0000000
Urabunana sericeivitta	0010000000	001000?010	0400100001	0101001100	0000???010	0110??1011	1?20201800	2001300000	0000??1011	1??1111111	1111110000	0?00000
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Head (characters 1–5, 88, 113)

Width of head is a character that has featured strongly in tribal and generic characterization and has been variously measured against the width of pronotum (e.g., Goding & Froggatt, 1904) and width of the mesonotum (e.g., Distant, 1906b; Boulard, 1996a; Liu, 1978). Development of the head is likely to be largely independent of thoracic development and is often variable between closely allied genera, e.g., *Diceropyga, Dilobopyga* and *Aceropyga* (Duffels, 1977), and even within a genus, e.g., *Tryella* (Moulds, 2003). For these reasons I have not followed traditional means of measuring head size. Instead, I have attempted to document the primary elements of head shape, *viz.* the lateral elongation of the vertex and postclypeus development.

1 *Head form*: (0) supra-antennal plate meeting or nearly meeting eye; (1) distance between supra-antennal plate and eye about equal to length of antennal plate; (2) vertex laterally elongate so that eyes widely separated from supra-antennal plate.

2 *Postclypeus shape in transverse cross-section*: (0) rounded; (1) angular.

3 *Postclypeus shape in lateral profile*: (0) rounded between "top" and "sides"; (1) angulate between "top" and "sides".

4 *Postclypeus ridges*: (0) ungrooved; (1) with transverse grooves towards distal ends.

5 *Antennal plate*: (0) rounded; (1) produced into a pointed lobe.

Thorax (characters 6–14, 94–97, 100)

6 *Pronotal collar width at dorsal midline*: (0) narrow, much less than diameter of eyes; (1) broad, equal to about diameter of eyes or greater; (2) very broad, equal to width of lateral angles.

7 *Pronotal collar lateral development*: (0) weakly ampliate or confluent with adjoining pronotal sclerites; (1) strongly ampliate, sloping in lateral view, evenly rounded in dorsal view; (2) strongly ampliate, horizontal in lateral view, evenly rounded in dorsal view; (3) strongly ampliate, horizontal in lateral view, tending triangular and pointed in dorsal view.

8 *Pronotal collar mid lateral tooth*: (0) absent; (1) present.

9 *Pronotal collar "file" on underside of lateral angles*: (0) absent; (1) present.

10 *Mesonotum with "file" on anterior angles* (Figs. 54, 55): (0) absent; (1) present.

11 *Cruciform elevation*: (0) wider than long; (1) narrower than long.

12 *Epimeral lobe*: (0) not reaching operculum; (1) reaching operculum.

13 *Metanotum*: (0) entirely concealed at dorsal midline; (1) partly visible at dorsal midline.

14 *Metanotum lateral area*: (0) not expanded over timbal; (1) expanded to partly cover timbal.

Wings (characters 15–34, 90, 98–99, 107–108)

Abnormalities in wing venation are common occurrences. Such abnormalities have been ignored when scoring character states.

Elongation of the basal cell has been used as a tribal character for the Dundubiini (Atkinson, 1886). While this application has an element of merit, it is difficult to interpret elongation from non-elongation. Elongation is closely linked with the meeting of veins M and CuA and the two trends are considered to be interdependent. For this reason only the association of veins M and CuA has been applied to the cladistic analysis.

15 *Fore wing apical cell number*: (0) 8 cells; (1) 9 cells; (2) 10 cells; (3) 12 cells; (4) 13 cells; (5) multiple reticulation; (6) 20 to more than 30 cells.

16 *Fore wing subapical cells*: (0) absent; (1) present.

17 *Fore wing subapical cell number*: (0) 4 cells; (1) c. 6 cells; (2) c. 20 cells.

18 *Fore wing ulnar cell 3* (Fig. 32): (0) angled to radial cell; (1) substantially parallel to radial cell.

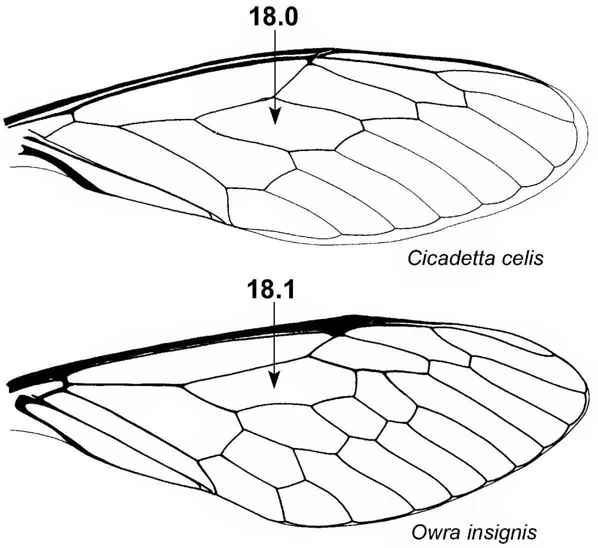


Fig. 32. Character 18. Fore wing ulnar cell 3, states 0 and 1: (*0*) angled to radial cell; (*1*) substantially parallel to radial cell.

19 *Fore wing costa*: (0) reducing or parallel-sided to node; (1) broadest a little before node; (2) with a swollen "nodule" preceding node.

20 *Fore wing pterostigma*: (0) present; (1) absent.

21 *Fore wing vein CuA*: (0) straight or weakly bowed so that cubital cell no larger than medial cell; (1) strongly bowed so that cubital cell much larger than medial cell.

22 *Fore wing veins M and CuA* (Fig. 33): (0) unfused and widely separated at basal cell; (1) unfused but CuA and M very much closer than CuA is to CuP+1A, with basal cell very elongate; (2) meeting at basal cell but veins not aligned; (3) meeting at basal cell with vein aligned after basal cell but not fused; (4) meeting basal cell with their stems completely fused.

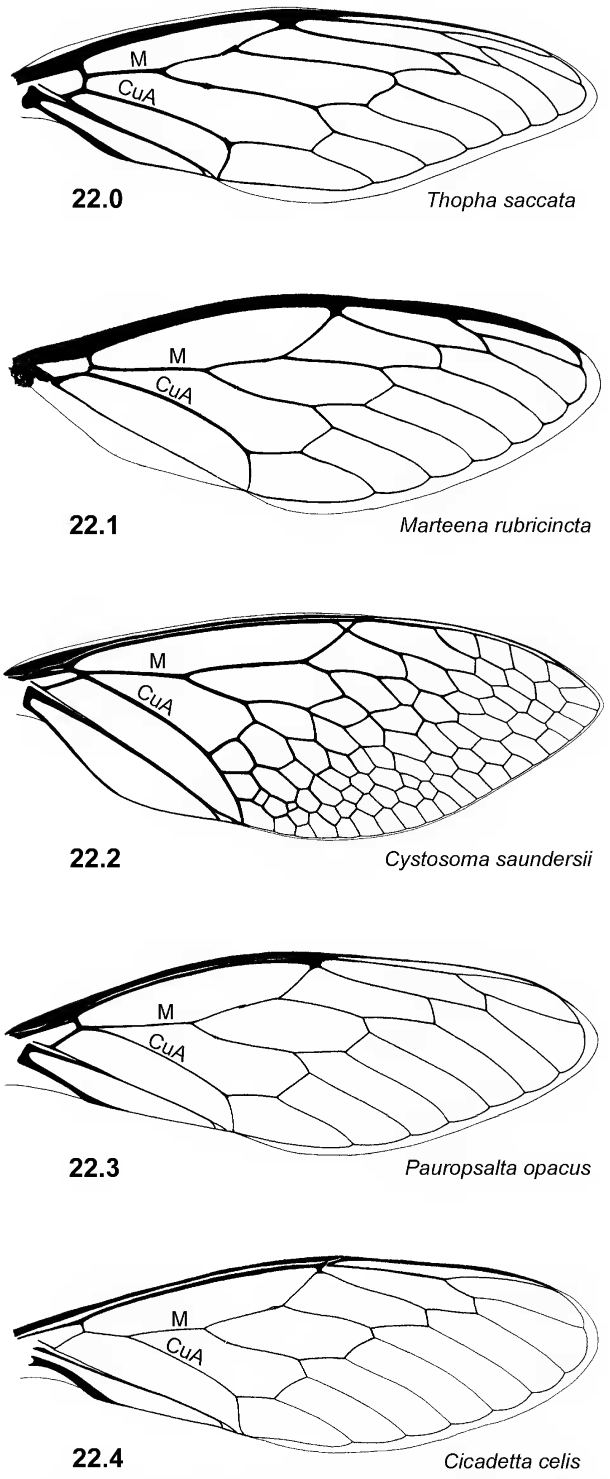


Fig. 33. Character 22. Fore wing veins M and CuA, states 0–4: (*0*) unfused and widely separated at basal cell; (*1*) unfused but CuA and M very much closer than CuA is to CuP+1A, with basal cell very elongate; (*2*) meeting at basal cell but veins not aligned; (*3*) meeting at basal cell with vein aligned after basal cell but not fused; (*4*) meeting basal cell with their stems completely fused.

23 *Fore wing vein RA_1*: (0) aligned closely with subcosta (Sc) for its length; (1) diverging from subcosta (Sc) in subapical region.

24 *Fore wing vein CuA_1*: (0) divided by crossvein so that proximal portion shortest; (1) divided by crossvein so that proximal portion longest. Those species where the division is nearly equal have been scored as unknown.

25 *Fore wing veins CuP and 1A*: (0) unfused; (1) fused at their bases.

26 *Fore wing veins C and R+Sc*: (0) close together; (1) widely separated.

27 *Fore wing outer margin* (Fig. 34): (0) developed for its total length; (1) greatly reduced and in part contiguous with ambient vein.

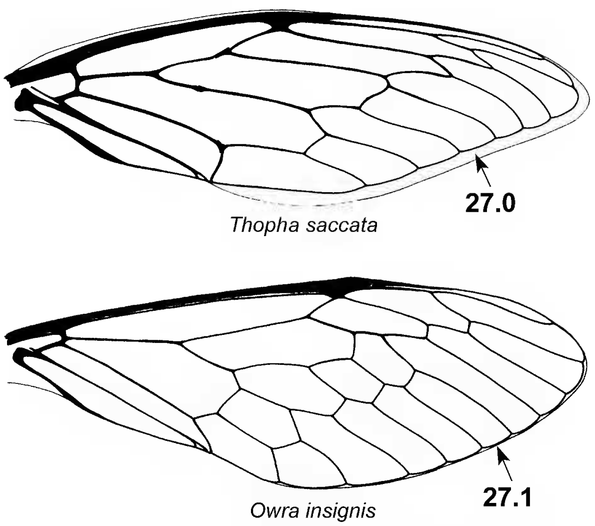


Fig. 34. Character 27. Fore wing outer margin, states 0 and 1: (*0*) developed for its total length; (*1*) greatly reduced and in part contiguous with ambient vein.

28 *Fore wing membrane*: (0) hyaline; (1) maculated, tegmen-like, opaque.

29 *Fore wing membrane when hyaline*: (0) lacking green tint; (1) with green tint.

30 *Hind wing apical cell number*: (0) 6 cells; (1) 4 or 5 cells; (2) 7–10 cells.

31 *Hind wing infuscation on wing margin at distal end of 2A*: (0) absent; (1) present.

32 *Hind wing 1st cubital cell width at distal end* (Fig. 35): (0) about equal to 2nd cubital cell; (1) much greater than 2nd cubital cell (twice or more).

33 *Hind wing anal lobe* (Fig. 36): (0) broad with vein 3A usually strongly curved at distal end, long and separated from wing margin; (1) narrow with vein 3A tending straight, short and usually adjacent to wing margin.

34 *Hind wing veins RP and M*: (0) unfused at base; (1) fused at base.

Legs (characters 35–36, 89, 109–110, 114–117)

35 *Fore leg femoral primary spine*: (0) erect; (1) lying flat, prostrate.

36 *Meracanthus*: (0) gradually tapering to a point, triangular or nearly so; (1)long, thin, parallel-sided, finger-like; (2) rudimentary, short, worm-like.

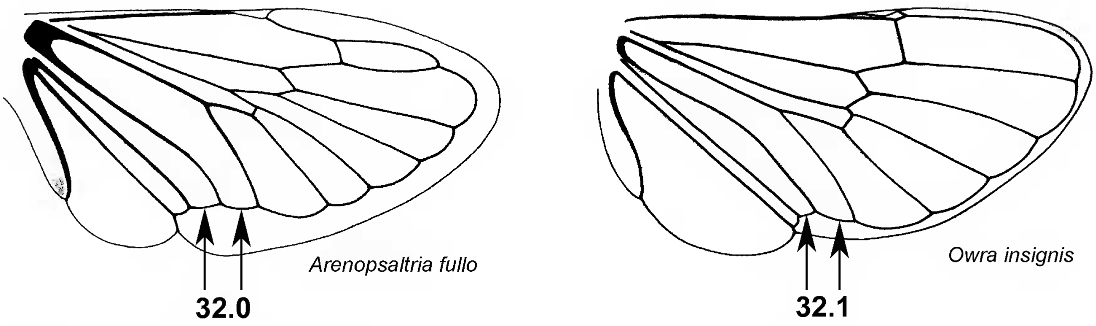


Fig. 35. Character 32. Hind wing 1st cubital cell width at distal ends, states 0 and 1: (*0*) about equal to 2nd cubital cell; (*1*) much greater than 2nd cubital cell (twice or more).

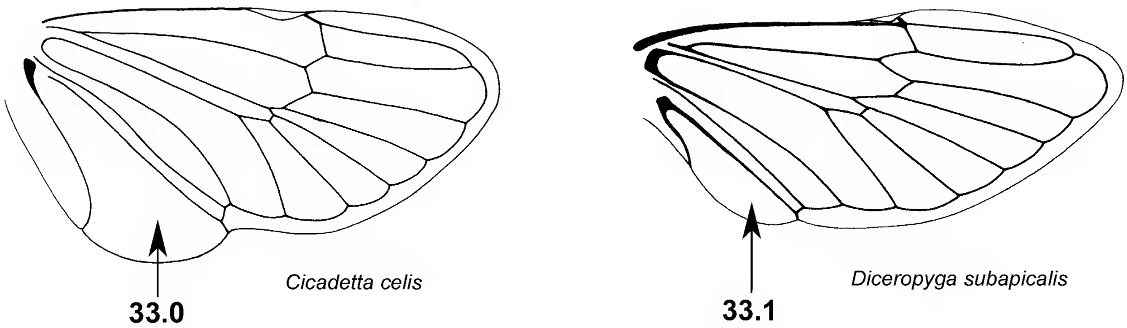


Fig. 36. Character 33. Hind wing anal lobe, states 0 and 1: (*0*) broad with vein 3A usually strongly curved at distal end, long and separated from wing margin; (*1*) narrow with vein 3A tending straight, short and usually adjacent to wing margin.

Male opercula (characters 37–38)

The apparent continuity of operculum development makes scoring difficult. Discrete groupings in length and breadth are for the most part lacking and distal and median development appear to be interrelated. For these reasons scoring of the opercula has been limited to identifying groupings exhibiting similar overall shape and size.

37 *Male opercula*: (0) lateral margin of operculum not raised above level of tympanal cavity margin; (1) lateral half of operculum raised above level of tympanal cavity.

38 *Male opercula development* (Fig. 37): (0) more or less confluent with distal margin of tympanal cavity, well developed towards abdominal midline with sharply rounded apices facing midline, clearly separated; (1) more or less reaching margin of tympanal cavity (rarely beyond), directed towards distomedial margin of tympanal cavity, apically broadly rounded, not meeting; (2) covering rim of distal margin of tympanal cavity, overlapping; (3) distant from lateral margin of tympanal cavity, directed towards distomedial margin of tympanal cavity, apically tapering to a blunt point, inner margin straight, clearly not meeting; (4) tending linear, both outer and inner margins straight or nearly so, distal margin broadly rounded, distally expanded towards midline, reaching distal margin of tympanal cavity or beyond, not meeting; (5) reaching far beyond tympanal cavity to cover some ⅔ length of abdomen, clearly separated; (6) completely covering tympanal cavity, completely encapsulating meracanthus, not overlapping; (7) nearly triangular, strongly cupped, covering and extending beyond tympanal cavity, completely encapsulating meracanthus, not meeting; (8) narrow, tending parallel-sided, lacking a distinct lateral angle, development towards abdominal midline, short of distal margin of tympanal cavity, far from meeting; (9) lateral margin arising considerably indented from basal extremity, partly encapsulating meracanthus, distal margin nearly straight, never closing tympanal cavity.

The scoring for *Aleeta* and *Birrima* is doubtful but are considered as extreme examples of state 4.

Abdomen (characters 39–43, 91, 101–102)

39 *Male tergites in cross-section*: (0) sides straight or convex; (1) sides partly concave.

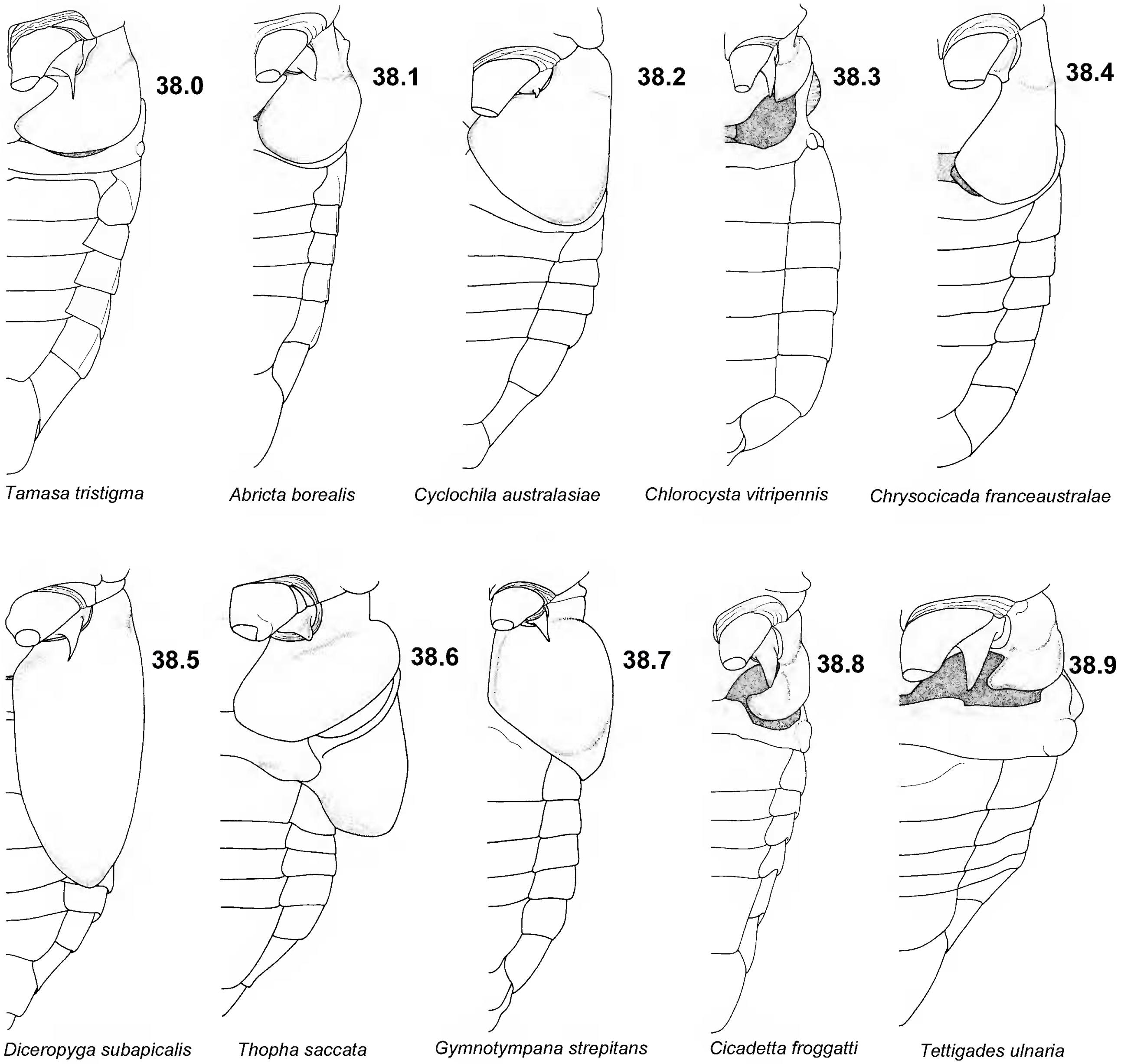
40 *Male tergites lateroventrally*: (0) epipleurites reflexed to ventral surface; (1) epipleurites rounded to ventral surface.

41 *Male tergites 2 and 3*: (0) similar in size to tergites 4–7; (1) much enlarged, 2+3 usually accounting for approximately half abdominal length.

Distinguishing these character states is not always clear cut and demarcation is somewhat arbitrary. The character, nevertheless, has been included because it is so dominant in some genera.

42 *Male epipleurites*: (0) straight or nearly so (1) epipleurite 4, and sometimes also others, strongly kinked inwards in a "V" shape.

43 *Male sternites in cross-section*: (0) 4–6 (and usually 7) convex; (1) flat except for upwardly tilted margin; (2) entirely flat.



Tamasa tristigma *Abricta borealis* *Cyclochila australasiae* *Chlorocysta vitripennis* *Chrysocicada franceaustralae*

Diceropyga subapicalis *Thopha saccata* *Gymnotympana strepitans* *Cicadetta froggatti* *Tettigades ulnaria*

Fig. 37. Character 38. Male opercula development, states 0–9: (*0*) more or less confluent with distal margin of tympanal cavity, well developed towards abdominal midline with sharply rounded apices facing midline, clearly separated; (*1*) more or less reaching margin of tympanal cavity (rarely beyond), directed towards distomedial margin of tympanal cavity, apically broadly rounded, not meeting; (*2*) covering rim of distal margin of tympanal cavity, overlapping; (*3*) distant from lateral margin of tympanal cavity, directed towards distomedial margin of tympanal cavity, apically tapering to a blunt point, inner margin straight, clearly not meeting; (*4*) tending linear, both outer and inner margins straight or nearly so, distal margin broadly rounded, distally expanded towards midline, reaching distal margin of tympanal cavity or beyond, not meeting; (*5*) reaching far beyond tympanal cavity to cover some ⅔ length of abdomen, clearly separated; (*6*) completely covering tympanal cavity, completely encapsulating meracanthus, not overlapping; (*7*) nearly triangular, strongly cupped, covering and extending beyond tympanal cavity, completely encapsulating meracanthus, not meeting; (*8*) narrow, tending parallel-sided, lacking a distinct lateral angle, development towards abdominal midline, short of distal margin of tympanal cavity, far from meeting; (*9*) lateral margin arising considerably indented from basal extremity, partly encapsulating meracanthus, distal margin nearly straight, never closing tympanal cavity.

Timbals and tympana (characters 44–49, 103–104)

44 *Rim of timbal cavity*: (0) lacking a turned-back rim or timbal cover; (1) with a turned-back rim; (2) developed as an anteriorly directed timbal cover.

Parnkalla has been scored as unknown. It shows minimal development of the timbal covers which exist only as a raised ridge directed neither forwards or backwards although it does differ from species lacking timbal covers in possessing an obvious tergal overhang of the timbal cavity. Boulard (1976a: 406) notes that the East African genus *Orapa* includes *O. elliotti* (Distant) with undeniable timbal covers but also *O. lateritia* Jacobi which appears to lack them, emphasizing the need for caution when scoring the presence/absence of timbal covers, where minimal development may be present.

45 *Timbal covers when present*: (0) flat; (1) swollen.

46 *Timbal covers when present*: (0) reduced dorsally and not reaching metathorax; (1) reduced dorsally and reaching metathorax; (2) fully rounded dorsally extending to metathorax but not tightly closing the timbal cavity; (3) fully rounded dorsally extending to metathorax and tightly closing the timbal cavity.

47 *Timbal covers when present*: (0) lower margin extending anteriorly from or very near auditory capsule; (1) lower margin extending vertically from auditory capsule before turning anteriorly.

48 *Timbal ribs*: (0) few, often irregular in size and usually spaced with prominent intermediate short ribs, very large basal dome; (1) many ribs regular in size and closely spaced filling entire timbal area apart from basal dome.

49 *Timbals*: (0) extended below wing bases; (1) not extended below wing bases.

Male external genitalia (characters 50–84, 105, 111)

The external genitalia comprise four main components; *pygofer, uncus, claspers* and *aedeagus* (Figs. 14–23).

Pygofer. The pygofer can carry up to three large lobes along each lateral margin. The *basal pygofer lobe* is considered to have originated from the 9th abdominal sternite and is likely homologous with the subgenital plate found in all other groups of Cicadomorpha and is always ventral to the pygofer *sclerital suture* (Fig. 14). The *upper pygofer lobe* is believed to be of tergal origin from the 9th segment and is always dorsal to the sclerital suture. The *distal shoulder* of the pygofer is extended in some genera to form a *lateral process* (*sensu* Duffels, 1977). Development of the distal shoulder is often associated with a dorsal beak that is not part of the chitinized pygofer but rather one that is attached as a flap to "hinge" membrane.

Uncus, uncal lobes and claspers. The *uncus* is the strongly sclerotized process originating adjacent to the median portion of the anal tube and usually (partly) covers the aedeagus. The anal tube and uncus together hinge basally and form the major part of the 10th abdominal segment (Figs. 14, 15). The uncus in some Cicadinae (e.g., Cosmopsaltriina) diverges into two arms, the *uncal lobes* (Fig. 44). These uncal lobes, with their bases originating from that part of the uncus adjacent to the median part of the anal tube, are considered not homologous with the claspers. The *claspers* are a pair of processes originating from below the uncus, on the basal part of segment 10 (Duffels & Turner, 2002). They are situated next to the aedeagus rather than above it. These are the prominent paired clasping organs holding the aedeagus in Cicadettini and Taphurini (Figs. 16, 17, 19, 20). In these tribes the uncus is reduced to a small duck-bill shaped lobe, the *uncal median lobe*. See also discussion of claspers under Character 61 below.

Aedeagus. The tubular shaft or *theca* attaches to a *basal plate*, and together these make up the *aedeagus*. The theca sometimes has one or more appendages, the origin of which often differs between tribes. Enclosed within the theca is the terminal part of the ejaculatory duct, the apical portion of which sometimes terminates in a fleshy endotheca and sometimes carries ornamentation. The endotheca in some species is invaginated and when extruded is called a *vesica*.

Strictly speaking, in Cicadidae (but not in Tettigarctidae) a true aedeagus is lacking and the basal plate (or connective) has been extended into a tubular elongation to form the theca. Only the Tettigarctidae retain a true aedeagus and basal plate (which are independent) as stated by Evans (1941).

50 *Pygofer distal shoulder* (Fig. 38): (0) not developed; (1) broad, rounded, often the most distal part of pygofer; (2) distally extended into pointed, and often apically up-turned, lobe.

51 *Pygofer inner tooth* (Fig. 39): (0) absent; (1) present.

52 *Pygofer upper lobe*: (0) absent; (1) present.

The pygofer upper lobe is here considered to be a lobe immediately dorsal of the pygofer sclerital suture (not to be confused with the distal shoulder; compare Figs. 38, 41).

53 *Pygofer upper lobe*: (0) thickened; (1) flat.

54 *Pygofer upper lobe when flat* (Fig. 40): (0) small to moderately developed, distant from dorsal beak, rounded; (1) very well developed, dominating pygofer between basal lobe and dorsal beak, very flat; (2) well developed, dominating pygofer between basal lobe and dorsal beak, concave on inner face; (3) moderately developed with accessory "tooth".

55 *Pygofer upper lobe when flat and very well developed*: (0) rounded or tapering; (1) expanded apically and shaped like a horse blinker.

56 *Pygofer upper lobe when thickened*: (0) well developed; (1) small, bud-like, accentuated by adjacent "dimple" in pygofer.

57 *Pygofer basal lobe*: (0) absent; (1) present, undivided; (2) present, plus a secondary basal lobe.

58 *Pygofer basal lobe development* (Fig. 41): (0) moderately developed, tending to be broadly rounded in lateral view; (1) ill-defined, substantially confluent with pygofer margin; (2) large, in lateral view projecting outwards, basically triangular but sometimes distally elongate; (3) large, in lateral view projecting outwards, linear, parallel-sided.

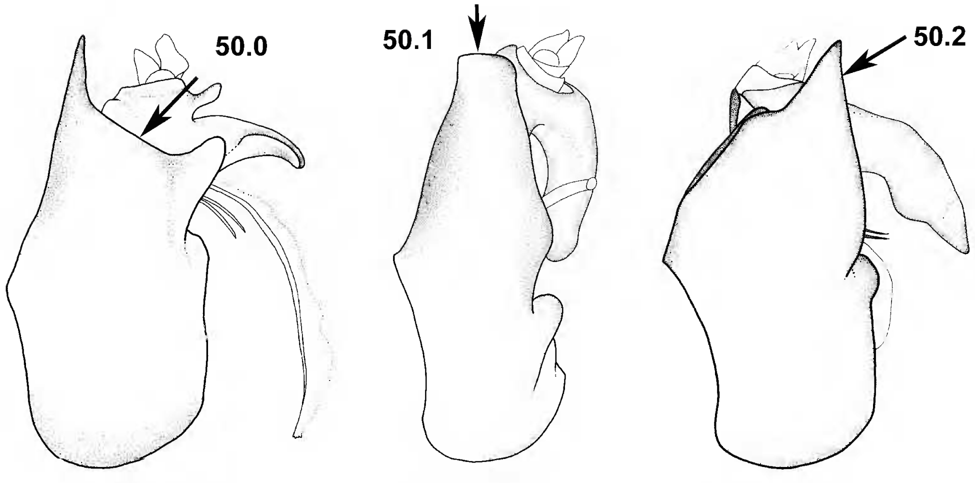
59 *Pygofer dorsal beak*: (0) absent; (1) present and a part of chitinized pygofer; (2) present but as a flap on "hinge" membrane.

Some individuals of *Cyclochila australasiae* lack a beak while others possess a small beak. *Cyclochila virens* always has a beak. Thus *C. australasiae* has been scored as possessing a beak.

60 *Ventrobasal pocket*: (0) present; (1) absent.

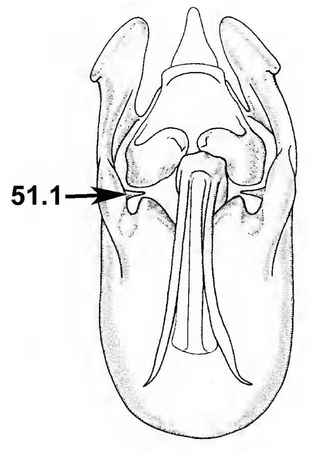
61 *Claspers*: (0) absent; (1) large, dominating the whole 10th abdominal segment; (2) small to medium sized, usually not dominating, spine apically.

Homologies for claspers remains a difficult issue. Many cicadas (e.g., many Cryptotympanini, and Platypleurini) possess small ventral lobes partly holding the aedeagus; these have been interpreted as not homologous with the claspers of either the Dundubiini or Tibicininae. In



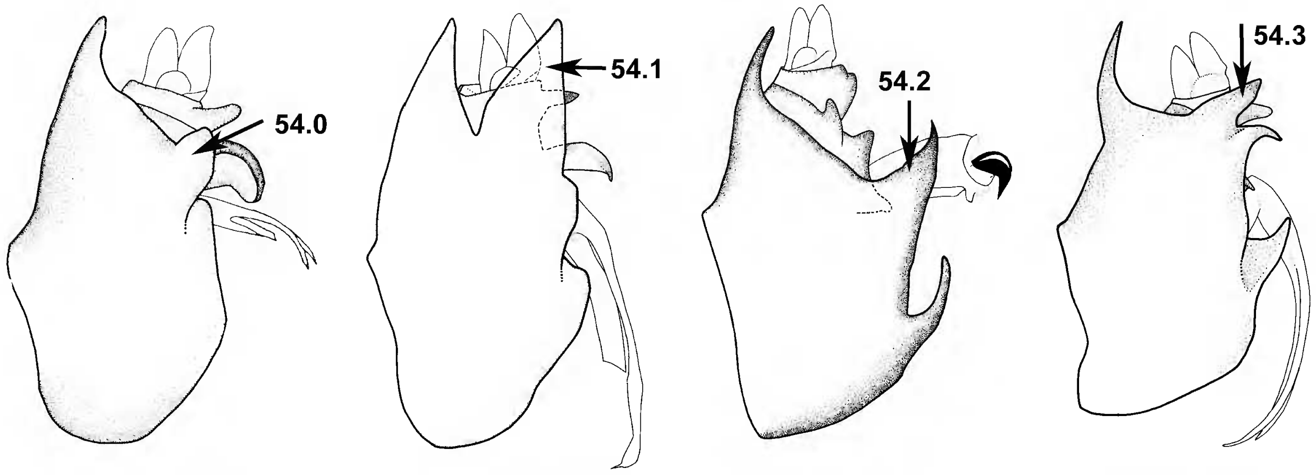
Birrima castanea *Anapsaltoda pulchra* *Cosmopsaltria doryca*

Fig. 38. Character 50. Pygofer in lateral view showing distal shoulder, states 0–2: (*0*) not developed; (*1*) broad, rounded, often the most distal part of pygofer; (*2*) distally extended into pointed, and often apically up-turned, lobe.



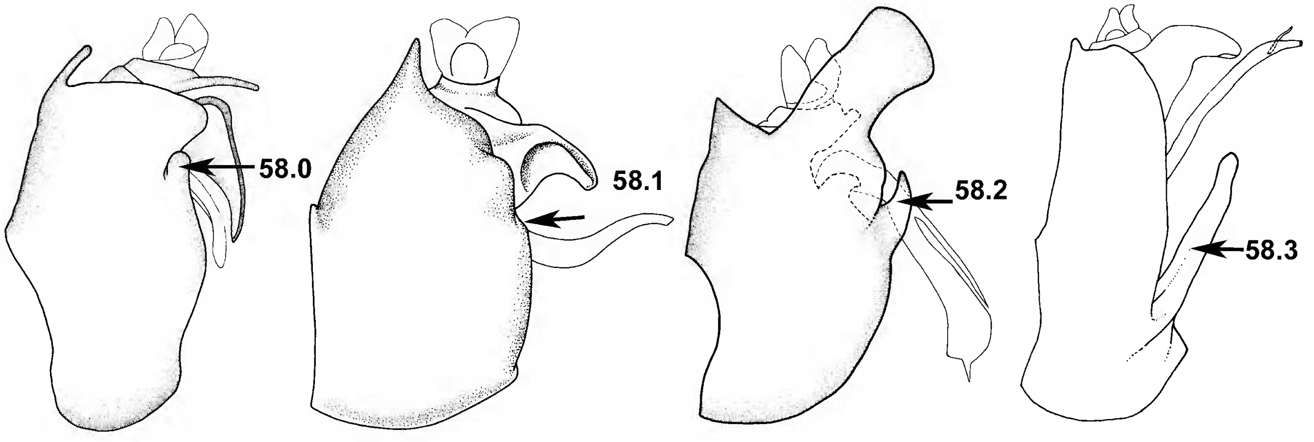
Pauropsalta encaustica

Fig. 39. Character 51. Pygofer in ventral view showing inner tooth, states 0–1: (*0*) absent; (*1*) present.



Diemeniana frenchi *Pauropsalta mneme* *Tryella ochra* *Pauropsalta basalis*

Fig. 40. Character 54. Pygofer in lateral view showing upper lobe when flat, states 0–3: (*0*) small to moderately developed, distant from dorsal beak, rounded; (*1*) very well developed, dominating pygofer between basal lobe and dorsal beak, very flat; (*2*) well developed, dominating pygofer between basal lobe and dorsal beak, concave on inner face; (*3*) moderately developed with accessory "tooth".



Urabunana sericeivitta *Glaucopsaltria viridis* *Pauropsalta eyrei* *Macrotristria angularis*

Fig. 41. Character 58. Pygofer basal lobe development, lateral view, states 0–3: (*0*) moderately developed, tending to be broadly rounded in lateral view; (*1*) ill-defined, substantially confluent with pygofer margin; (*2*) large, in lateral view projecting outwards, basically triangular but sometimes distally elongate; (*3*) large, in lateral view projecting outwards, linear, parallel-sided.

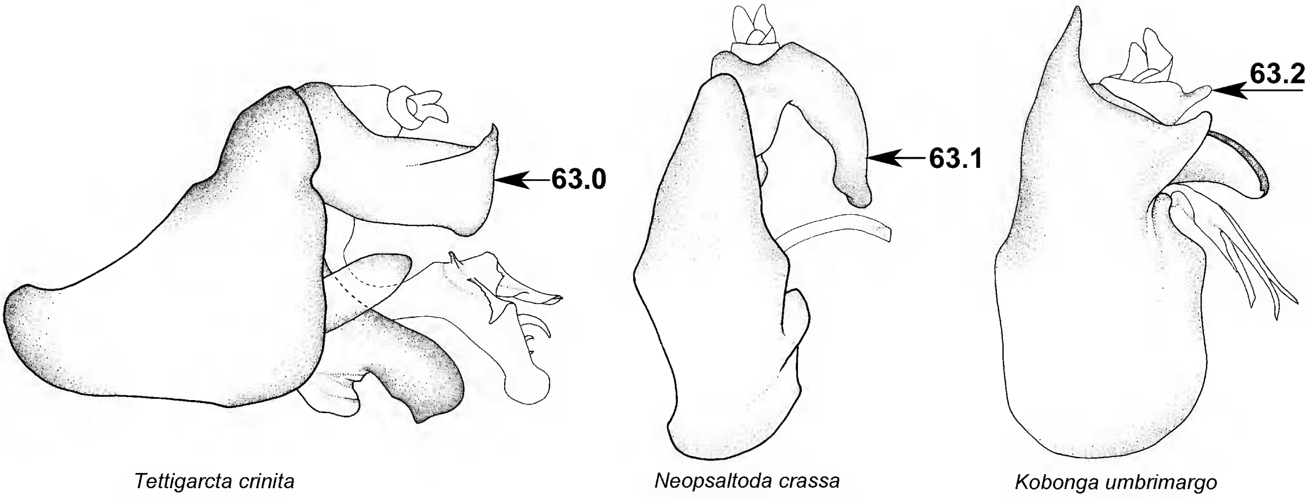


Fig. 42. Character 63. Uncal shape, lateral view, states 0–2: (*0*) n-shaped in cross-section, apically with sides meeting but not fused; (*1*) digitate or basically tubular, large, dominant; (*2*) duck-bill shaped, small and flat, not dominant; (*3*) absent.

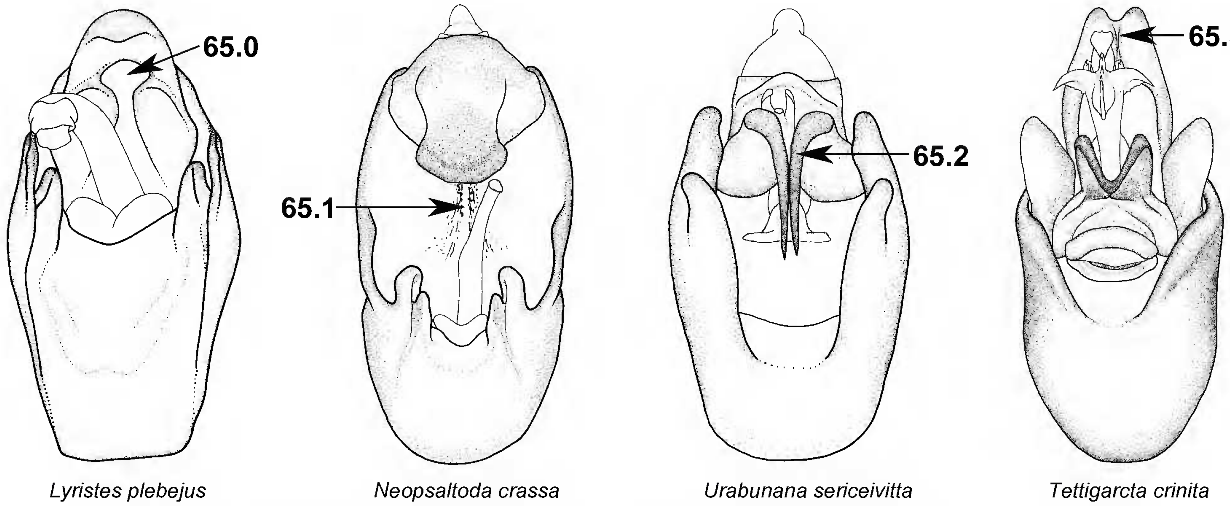


Fig. 43. Character 65. Uncal aedeagal restraint, states 0–3: (*0*) by tubular encapsulation on ventral surface of uncus; (*1*) by membrane prior to ventral surface of uncus; (*2*) by claspers; (*3*) by apical slit in uncus.

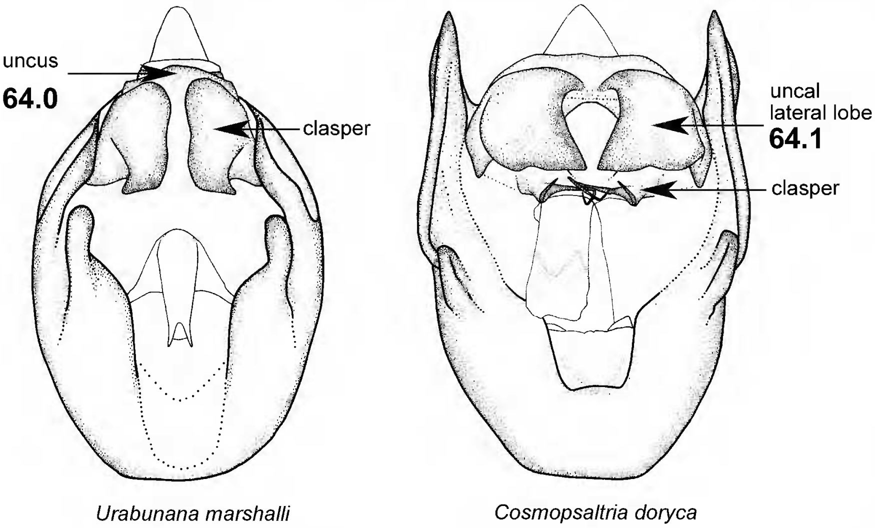


Fig. 44. Character 64. Uncal lateral lobes, states 0 and 1: (*0*) absent; (*1*) present.

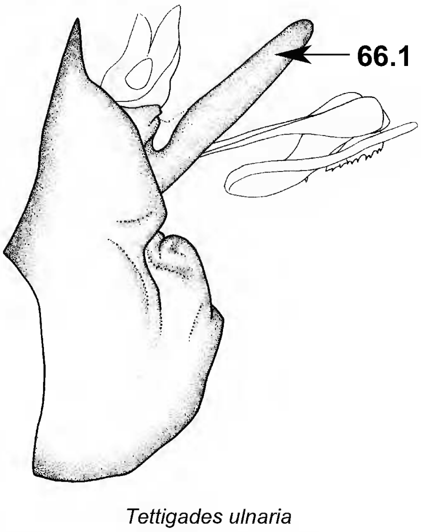


Fig. 45. Character 66. Uncal length, states 0 and 1: (*0*) of moderate proportions, retractable within pygofer; (*1*) exceedingly long, non-retractable within pygofer.

fact, these lobes may themselves not be all homologous.

See also comments on claspers under the heading "Male genitalia" above.

62 *Clasper separation*: (0) closely aligned; (1) widely separated.

63 *Uncal shape* (Fig. 42): (0) n-shaped in cross-section, apically with sides meeting but not fused; (1) digitate or basically tubular, large, dominant; (2) duck-bill shaped, small and flat, not dominant; (3) absent.

For comments on the uncus see "Male genitalia" above.

64 *Uncal lateral lobes* (Fig. 44): (0) absent; (1) present.

The uncal lateral lobes, the result of a deeply divided uncus (a structure originating from the anterior part of the anal tube as discussed above under the heading "Male genitalia"), are not the uncal lobes often ascribed previously to the Taphurini and Cicadettini, the latter structures are better termed claspers as they are considered to be of a different origin from the uncus and possibly homologous with the claspers of Duffels (1977) as found in some Dundubiini.

65 *Uncal aedeagal restraint* (Fig. 43): (0) by tubular encapsulation on ventral surface of uncus; (1) by membrane prior to ventral surface of uncus; (2) by claspers; (3) by apical slit in uncus.

66 *Uncal length* (Fig. 45): (0) of moderate proportions, retractable within pygofer; (1) exceedingly long, non-retractable within pygofer.

67 *Aedeagal basal plate in lateral view* (Fig. 46): (0) right-angled at distal end; (1) undulated, weakly depressed on dorsal midline; (2) sharply turned through more than 90°; (3) downturned at distal end; (4) basally very narrow becoming broad apically.

68 *Aedeagal basal plate in dorsal view* (Fig. 47): (0) parallel-sided, basal two-thirds without sclerotization except laterally; (1) apically broadened with "ears"; (2) basally divided into two discs, apical arms lobe-like; (3) deeply divided into two arms; (4) midline deeply furrowed, apically square or bilobed; (5) short, broad, usually rounded; (6) T-shaped; (7) Y-shaped; (8) broad, triangular with anterior angles elongate; (9) broad, apically broadly bilobed.

Those genera with a unique basal plate shape (*Cosmopsaltria, Diceropyga, Taphura, Venustria* and that represented by *Cicadetta forresti*) have been scored as "?".

69 *Aedeagal basal plate*: (0) basal portion directed forwards away from thecal shaft; (1) basal portion directed upwards nearly parallel with thecal shaft.

70 *Aedeagal basal plate ventral rib* (Fig. 48): (0) completely fused with basal plate; (1) rod-like, suspended with attachment only at ends.

71 *Aedeagal basal plate attachment* (Fig. 49): (0) entirely membranous, loosely attached; (1) completely chitinous with no mobility; (2) with a functional membranous "hinge".

72 *Aedeagal basal hinge when present*: (0) small, substantially compressed between theca and basal plate in lateral view; (1) large, highly visible in lateral view.

73 *Theca in lateral view*: (0) straight or curved in a gentle arc; (1) recurved basally through 180° or more, J-shaped or spiralled; (2) "S" shaped; (3) recurved basally through some 90–140°; (4) spiralled.

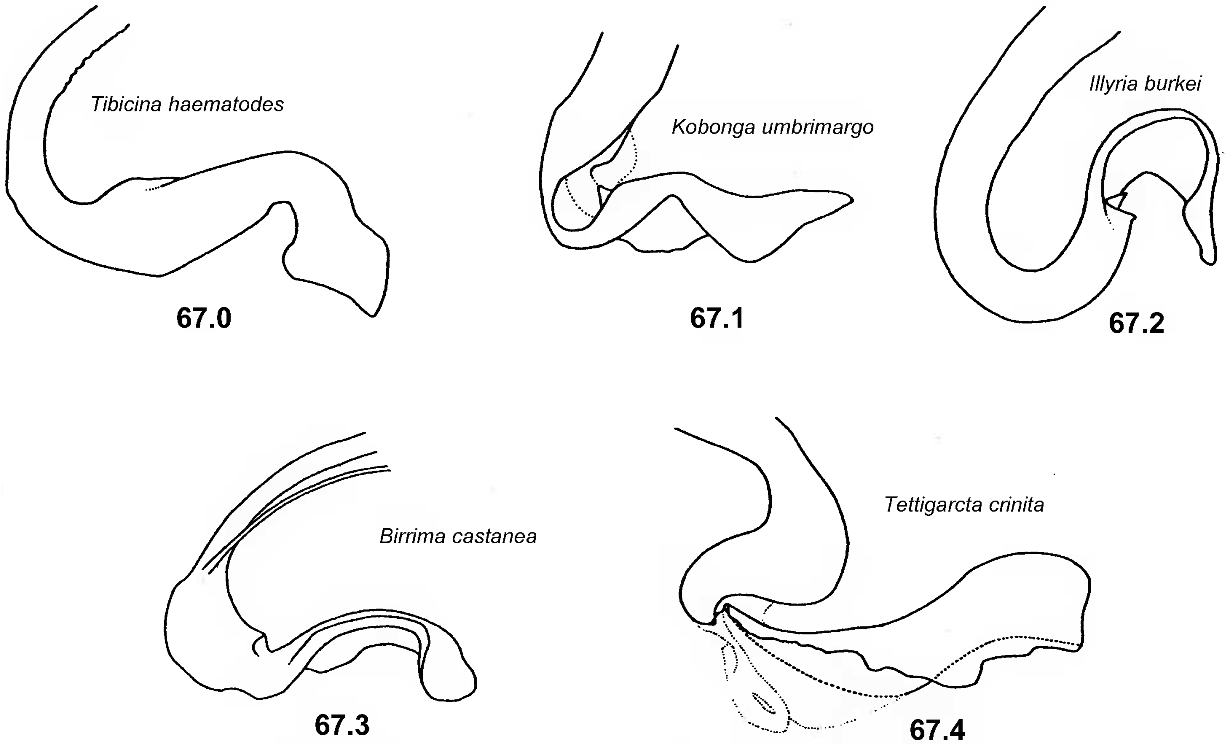


Fig. 46. Character 67. Aedeagus basal plate in lateral view, states 0–4: (*0*) right-angled at distal end; (*1*) undulated, weakly depressed on dorsal midline; (*2*) sharply turned through more than 90°; (*3*) downturned at distal end; (*4*) basally very narrow becoming broad apically.

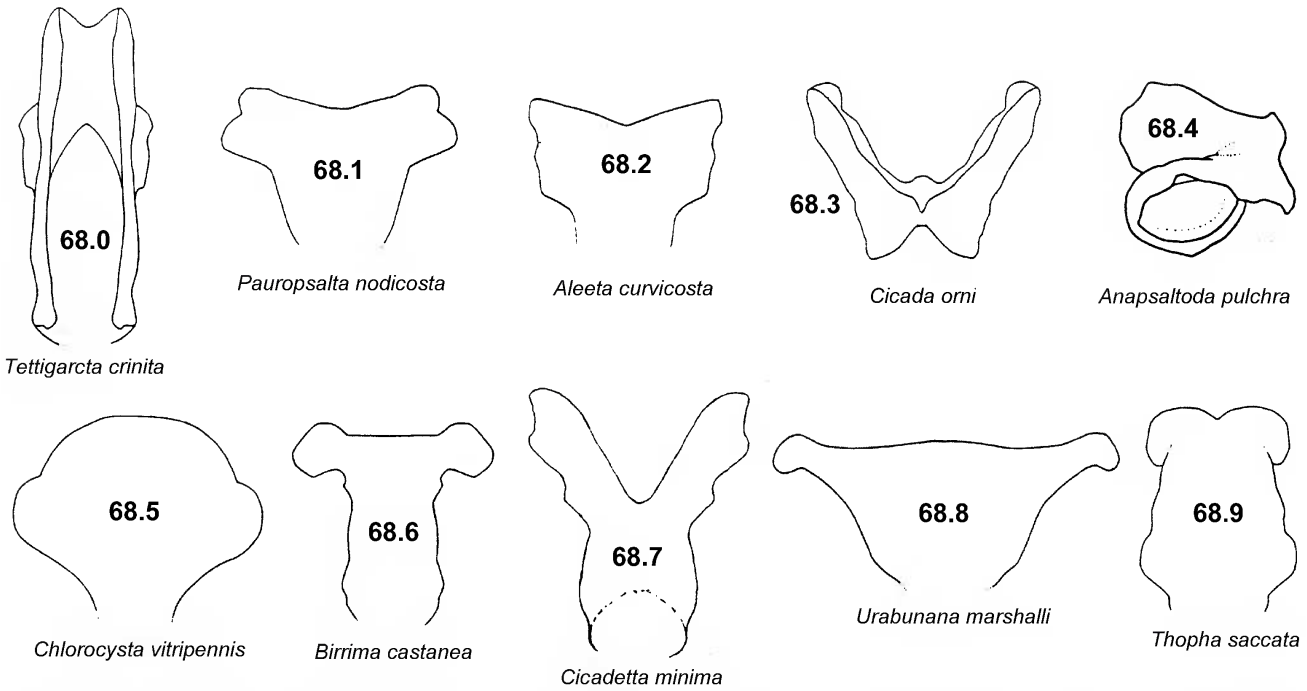


Fig. 47. Character 68. Aedeagal basal plate in dorsal view (apex at top), states 0–9: (*0*) parallel-sided, basal two-thirds without sclerotization except laterally; (*1*) apically broadened with "ears"; (*2*) basally divided into two discs, apical arms lobe-like; (*3*) deeply divided into two arms; (*4*) midline deeply furrowed, apically square or bilobed (dorsolateral view); (*5*) short, broad, usually rounded; (*6*) T-shaped; (*7*) Y-shaped; (*8*) broad, triangular with anterior angles elongate; (*9*) broad, apically broadly bilobed.

74 *Thecal pseudoparameres*: (0) absent; (1) present.

75 *Thecal pseudoparameres* (Fig. 50): (0) dorsal of theca, originating closer to apex of theca than its base, always much longer than theca; (1) dorsal of theca, originating near thecal base; (2) lateral of theca, filiform or flat and usually very long; (3) lateral of theca, dorsally fused to near their apices.

76 *Endothecal ventral support*: (0) absent; (1) present.

77 *Endotheca*: (0) in part or entirely chitinized; (1) entirely fleshy.

78 *Apical part of theca*: (0) entirely chitinized; (1) partly or entirely fleshy.

79 *Apical part of theca* (Fig. 51): (0) without leaf-like lobes; (1) with a pair of leaf-like lateral lobes.

80 *Vesica*: (0) tending to be amorphous, never long and tubular; (1) as a long thin, parallel-sided tube.

81 *Vesica opening on theca*: (0) apical; (1) dorsal.

82 *Thecal subapical cerci*: (0) absent; (1) present.

83 *Thecal flabellum*: (0) absent; (1) present.

84 *Thecal conjunctival claws*: (0) absent; (1) present.

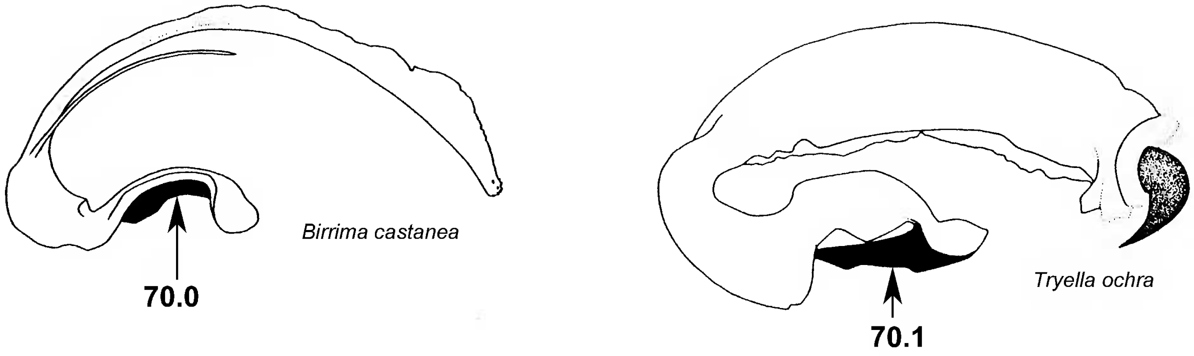


Fig. 48. Character 70. Aedeagal basal plate in lateral view showing ventral rib, states 0 and 1: (*0*) completely fused with basal plate; (*1*) rod-like, suspended with attachment only at ends.

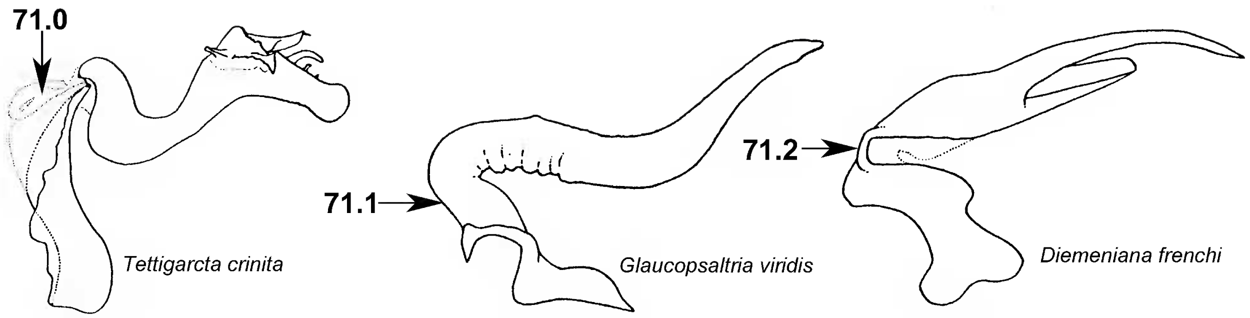


Fig. 49. Character 71. Basal plate attachment, states 0–2: (*0*) entirely membranous, loosely attached; (*1*) completely fused with no mobility; (*2*) with a functional membranous "hinge".

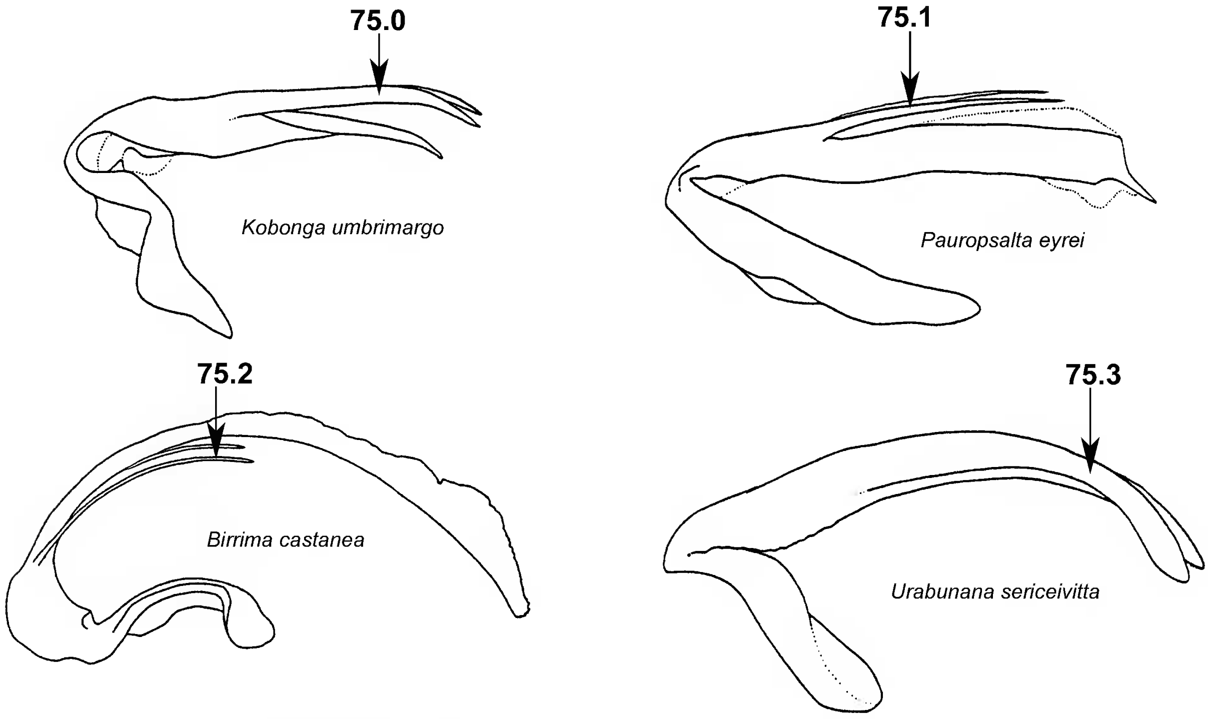


Fig. 50. Character 75. Thecal pseudoparameres, states 0–3: (*0*) dorsal of theca, originating closer to theca than its base, always much longer than theca; (*1*) dorsal of theca, originating near thecal base; (*2*) entirely lateral of theca, filiform or flat and usually very long; (*3*) lateral of theca, dorsally fused to near their apices.

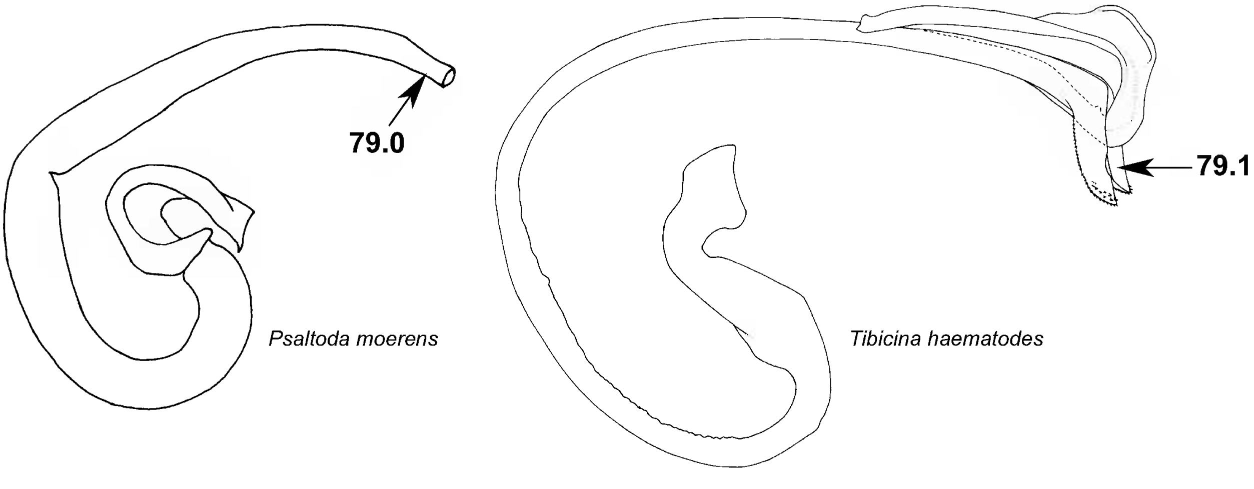


Fig. 51. Character 79. Apical part of theca, states 0 and 1: (*0*) without leaf-like lobes; (*1*) with a pair of leaf-like lateral lobes.

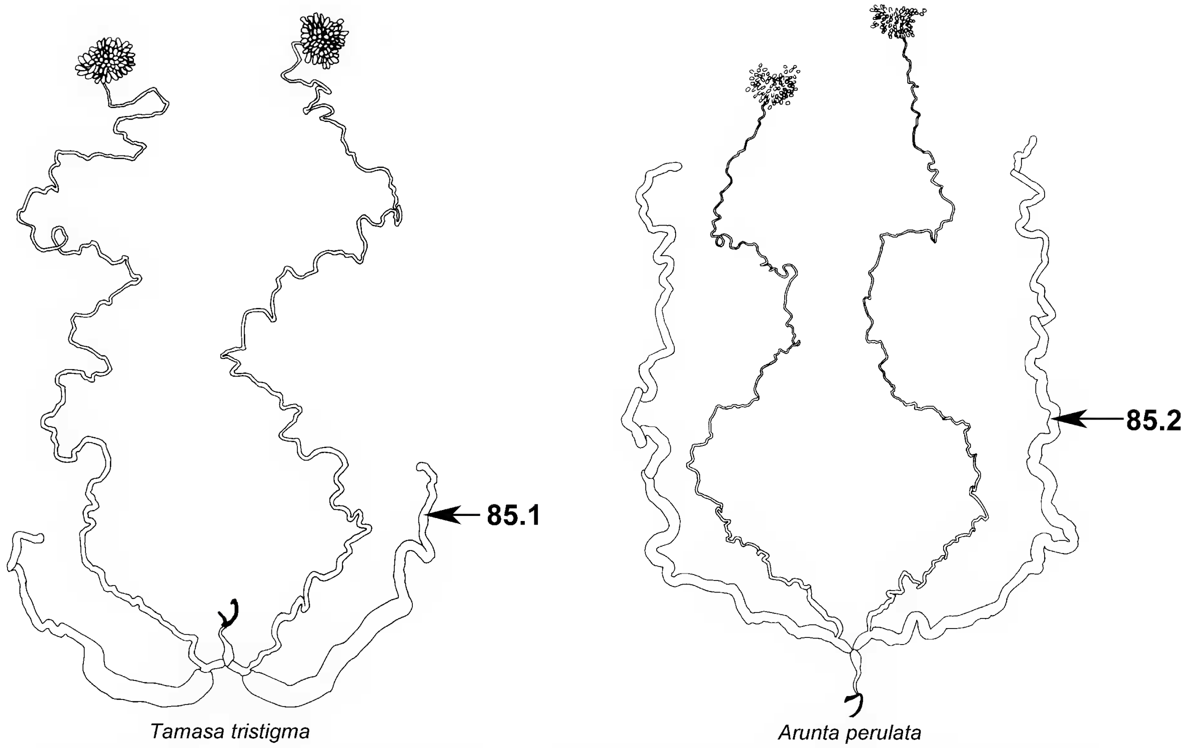


Fig. 52. Character 85. Male reproductive system, accessory glands, states 0–2: (*0*) absent; (*1*) short; (*2*) long.

Male reproductive system (characters 85, 93, 106)

There has been no previous comparative study of internal male reproductive systems. Multiple dissections of 23 species representing 19 genera spread over the three primary Australian lineages revealed two discrete groupings, those with short accessory glands and those with long accessory glands. No intermediates were found. The secondary accessory gland figured by Carver *et al.* (1991) for a *Cicadetta* species is dismissed as erroneous.

85 *Accessory glands* (Fig. 52): (0) short; (1) long.

Female reproductive system (characters 86–87, 92, 112)

Torres (1963) drew attention to the taxonomic value of the female internal reproductive system of Cicadidae. Boulard (1965) confirmed the ditrysian nature of many female cicadas and of some other Auchenorrhyncha (i.e. they possess two genital apertures, one for copulation, the other for egg deposition), substantiating Doyère's (1837) original discovery of two apertures in *Fidicina* (not *Tibicina* as stated by Matsuda, 1976). However, Boulard found that cicadas of the genera *Tettigarcta* and *Tettigades* were monotrysian (one genital opening). The ditrysian condition is also widespread in the Fulgoromorpha (Bourgoin, 1993) (Bourgoin & Huang, 1991) although some genera of tropiduchids remain monotrysian. Bourgoin & Huang (1991) recognized three differing ditrysian conditions and believed that they evolved independently several times. They added that in fulgorids and dictyopharids the ditrysian condition may have arisen as it has in cicadas where in mature nymphs the developing gonapophyses VII secondarily divide the single opening to the ovipositor (Boulard, 1990).

It is interesting to note that J.G. Myers (1928, 1929) states that he could not find the spermathecal gland in either *Carineta formosa* (now *C. diardi*) or *Melampsalta scutellaris* (now *Kikihia scutellaris*) although he did locate all other structures including the very delicate filamentous glands. The spermathecal gland certainly is present in *Kikihia* spp. (pers. obs.) and is most likely also present in *Carineta*; it is present in all other cicadas examined, including *Tettigarcta*, and the loss of such a major gland would be a radical loss indeed.

Gadd (1910) compared the female reproductive systems of the Palaearctic species *Lyristes plebejus, Cicada orni, Psalmocharias querula, Cicadatra atra, C. hyalina, Cicadetta podolica* and *C. montana*. He found that the spermathecal gland in *L. plebejus* and *C. orni* (tribes Cryptotympanini and Cicadini respectively) was very long, while in *Cicadatra* (tribe Cicadettini) it was reduced and in *Cicadetta* (also Cicadettini) it was much shorter than the oviduct. While I have not been able to confirm these differences, I did find amongst Australian Cicadettini that the spermathecal gland was somewhat shorter in *Pauropsalta mneme* but not in *Cicadetta labeculata* and *C. tristrigata*. Scoring these differences in length for the cladistic analyses was rejected as no clear groupings were evident. However, the lengths of the accessory glands of the common oviduct appeared more polarized and these were included although I would not be surprised if additional dissections eventually revealed intermediates.

Boulard (1973a) and Dugdale (1972) gave special emphasis to the carrefour region of the female genitalia, deriving generic diagnostic characters from dissections prepared from dried specimens. I found considerable distortion and decomposition of the reproductive system in dried specimens and consequently confined my study to examination of freshly killed specimens. I was unable to relate the finding of the above authors to dissections prepared from freshly killed specimens and consequently I have not adopted their conclusions.

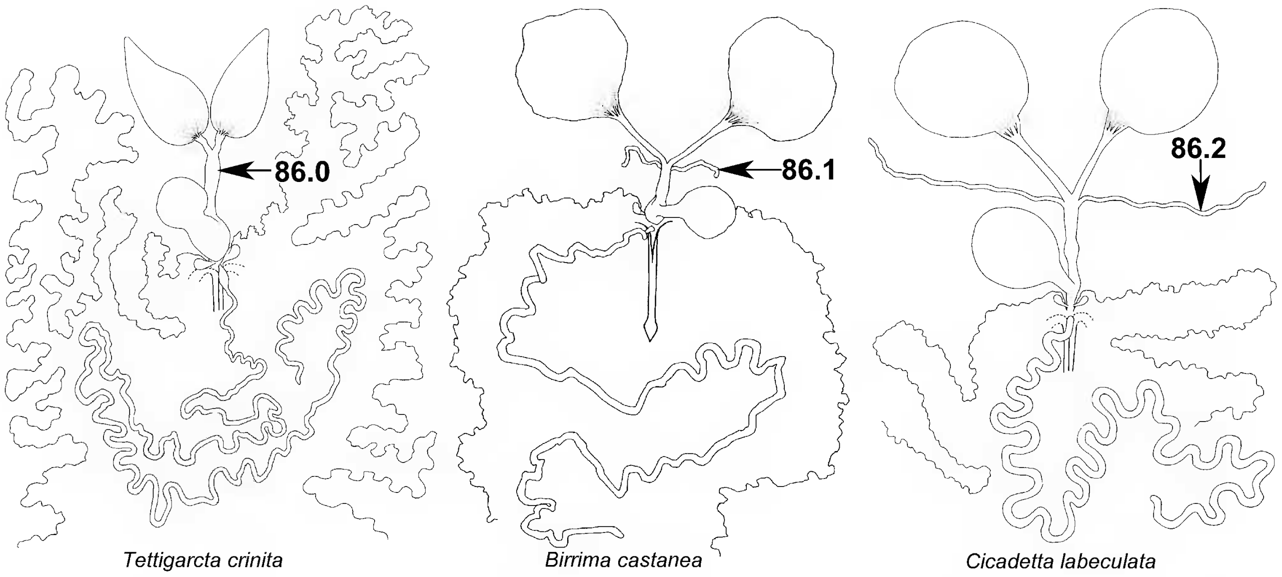


Fig. 53. Character 86. Female reproductive system, accessory glands of common oviduct, states 0–2: (*0*) absent; (*1*) short; (*2*) long.

86 *Accessory glands of common oviduct* (Fig. 53): (0) absent; (1) short; (2) long.

87 *Genital apertures*: (0) monotrysian; (1) ditrysian.

Characters diagnostic for Cicadoidea

88 *Ocelli*: (0) 3; (1) 2, or none.

89 *Fore femora*: (0) normal; (1) thickened.

90 *Hind wing membrane*: (0) numerous microtrichia; (1) no microtrichia.

91 *Male subgenital plate*: (0) present (1) lacking.

92 *Female reproduction system*: (0) no reservoir at base of filamentous glands; (1) reservoir present.

93 *Male reproduction system*: (0) few testicular follicles (c. 17); (1) numerous testicular follicles (perhaps 100 or more).

Characters diagnostic for Cicadidae

94 *Pronotal development*: (0) exceedingly large and concealing majority of mesonotum; (1) smaller than mesonotum.

95 *Pronotum paramedian and lateral fissures*: (0) absent; (1) present.

96 *Pronotal collar*: (0) absent; (1) present.

97 *Mesonotum*: (0) with a scutellum; (1) with a cruciform elevation.

98 *Fore wing veins 2A and 3A*: (0) unfused; (1) fused for much of their length.

99 *Hind wing hamulus*: (0) present; (1) absent.

100 *Thoracic ganglia*: (0) separated; (1) fused.

101 *Sternite VIII*: (0) not shielding genitalia; (1) shielding genitalia ventrally.

102 *Male abdominal resonant chamber*: (0) absent; (1) present.

103 *Tympana*: (0) absent; (1) present.

104 *Female timbals*: (0) present; (1) absent.

105 *Male genital styles*: (0) present; (1) absent.

106 *Testes*: (0) located anteriorly, centred over abdominal sternites II–III; (1) located posteriorly, centred over abdominal sternite VI.

Characters diagnostic for Tettigarctidae

107 *Fore wing vein RP*: (0) arising from node; (1) arising near wing base.

108 *Fore wing nodal line*: (0) indistinct; (1) well developed.

109 *Pretarsal empodia*: (0) absent; (1) present.

110 *Hind coxae*: (0) not overhanging abdomen; (1) overhanging abdomen.

111 *Aedeagal subapical sclerotized dorsal crest*: (0) absent; (1) present.

112 *Female accessory glands of common oviduct*: (0) present; (1) absent.

113 *Nymphal antennae*: (0) segments 1 and 2 together longer than segment 5; (1) segments 1 (scape) and 2 (pedicel) both very short and together equal segment 5 (3rd flagellomere).

Segments 1 and 2 have been compared with segment 5 as segments 3 and 4 are modified in some genera.

114 *Nymphal fore femora*: (0) no mid-lateral spine; (1) with a mid-lateral stout spine on outer face.

115 *Nymphal fore tibiae*: (0) subapical tooth absent or weakly developed and not opposing apical tooth; (1) a large subapical tooth opposing apical tooth.

116 *Nymphal mid and hind tibiae*: (0) no spines along shank; (1) with two stout spines along shank, one each at about ⅓ intervals.

117 *Nymphal hind tibiae*: (0) spinal crown with all spines similar; (1) spinal crown including one very dominant flat spine.

Results and discussion

Analysis produced 634 most parsimonious trees (although 94 of these were duplicate topologies), with a length of 295 steps, a consistency index (CI) of 0.58, and a retention index (RI) of 0.89. The strict consensus tree (Fig. 56) revealed that it was the placement of twig genera only that differed. The 634 trees do not differ in any major aspect in how they suggest character transformations (Figs. 59–62).

Consistency indices

The consistency index (CI) provides the measure of fit of characters to a tree (Kluge & Farris, 1969). The CI of 0.58 is above that empirically expected under a null model of no hierarchical structure. There is an inverse relationship between a CI and the number of taxa analysed (Sanderson & Donoghue, 1989; Doyen, 1993). Sanderson & Donoghue give the expected CI for 60 taxa as 0.347. Here I analyse 81 taxa so the CI is higher than expected had there been no hierarchic pattern in the data.

The retention index (RI) gives the fraction of apparent synapomorphy for the characters that are retained as such on the tree (Farris, 1989b). Like the CI, the RI of 0.89 is correspondingly strong.

Robustness of clades

Jackknife and T-PTP analyses were used to assess the robustness of clades. Like all other tests of robustness, the results must be viewed with caution as there are several ways in which either the data or the method might mislead. Most of the key nodes of interest (Fig. 56) are well supported by the data although a few others show poor support.

It should also be noted that just a single character at a twig can provide 100% jackknife support but more than one is essential at basal nodes for similar support, and the more taxa included the greater the need for characters at basal nodes. The result of a 50% jackknife analysis and T-PTP scores (significant at $P = < 0.05$) are given in Fig. 56.

Some notable character trends

The following trends result from unordered character transformations. Numbered clades mentioned in the text refer to Fig. 56.

Head width. Problems with judging head width against the width of the pronotum have been discussed above under "Characters". A perceived narrowing of the head (or more accurately extreme shortening of the vertex) always occurs as a derived condition (apomorphic) within the family Cicadidae (e.g., in some Cicadini, Plautillini, Chlorocystini, Prasiini). The narrow head of *Tettigarcta*, family Tettigarctidae, may also be apomorphic but this cannot be determined from the analysis (which supports plesiomorphy) because the branch lacks knowledge on close ancestors; however, Shcherbakov (in prep.) suggests that the narrow head of *Tettigarcta* could well be a derived condition that is possibly confined to *Tettigarcta* as the Cenozoic tettigarctid, *Tettigambra mouldsi*, is "quite large-headed". The narrowed head of *Plautilla* (and its allies), likewise, is probably apomorphic. All these taxa with very narrow heads possess other apomorphies (e.g., a very narrow hind wing anal lobe, elongate basal cell, a prostrate fore leg primary spine and a modified abdomen) which support the likelihood of a very narrow head being always apomorphic.

Widening of the head (or more accurately, elongation of the vertex, character state 1.2) is also an apomorphic condition in some genera. In clade 4 it is pronounced in the genus *Thopha* which also has highly modified male timbal covers and in two allied clades, one comprising *Psaltoda, Neopsaltoda* and *Anapsaltoda* and the other *Lyristes* and *Cryptotympana*. Within clade 5, the sister group of clade 4, a group of species comprising *Cicadetta minima, C. graminis, Pauropsalta basalis, P. eyrei* and *P.* sp. M, also possesses a wide head clearly wider than those of allied clades but not as pronounced as those genera of clade 4. No doubt there are other examples to be found in genera not included in this analysis. The analysis shows no reversing of trends in head width, i.e. head narrowing followed by head widening, or vice versa.

Fore wing vein M and CuA. The tendency towards fusion of fore wing veins M and CuA adjacent to the basal cell is a feature evident in all major clades. These veins show degrees of proximity without fusion in clade 6 (*Plautilla*), clade 18 (*Dundubia, Diceropyga, Cosmopsaltria, Tamasa, Parnkalla, Psaltoda* and *Neopsaltoda*), clade 8 (*Taphura*) and in clade 12 (*Cystosoma* and *Venustria*). Total fusion (character state 22.4) occurs only in clade 13 (the Cicadettini) but notably in three sister subclades, or in other words on three separate occasions; in clade 14 these veins only just meet in *Cicadetta montana* but are totally fused in the remaining taxa, in clade 16 which includes several genera where these veins are totally unfused as well as genera where fusion is complete, and in clade 17 with the genus *Pauropsalta* having species lacking fusion (not included in this analysis) as well as others with fusion while all other genera in the clade have total fusion.

Near or total fusion of veins M and CuA always appears as a derived condition. Clade 13 suggests that the fusion of M and CuA reverses on two occasions. This is an unlikely situation and arrangements within clade 13 should be viewed with caution; nodes within the clade are not well supported.

Elongation of the basal cell always occurs in association with the merging of veins M and CuA. This is apparently caused by the migration of CuA towards M and never M towards CuA.

Hind wing anal lobe. A narrow anal hind wing lobe (character state 33.1) occurs independently in five clades, in *Zammara, Odopoea* and *Plautilla* (clade 6), in the Prasiini represented by *Lembeja* and *Prasia* (clade 10), in the Cosmopsaltriina represented by *Diceropyga* and *Cosmopsaltria* (a part of clade 22), in the Platypleurini represented by *Platypleura* and *Oxypleura* (clade 26), and in *Gymnotympana* (a part of clade 12). All these groupings comprise species that possess other features that suggest they are highly modified. The most narrow anal lobes occur in *Plautilla, Zammara*, the Prasiini and *Gymnotympana strepitans*; all show other marked modifications. Thus, the narrower an anal lobe is, the more derived the species is likely to be. The cladistic analysis shows no reversal of this trend.

Fore leg primary spine. A prostrate fore femoral primary spine (character state 35.1) is found in four widely separated clades; in *Oxypleura* and *Platypleura* (clade 26), in *Thaumastopsaltria,* *Cystosoma* and *Cystopsaltria* (a subclade of clade 12), in *Plautilla, Zammara* and *Odopoea* (clade 6), and in *Tettigarcta* (clade 1). There is no reversal of this trend and the attribute is most likely indicative of an advanced condition. However, in *Tettigarcta* the analysis shows it is a plesiomorphy but a lack of knowledge of close ancestors may be the cause of this (see discussion under *Head width* above).

Male opercula. Moulton (1923: 76) believed that the opercula (like the timbal covers) are a comparatively recent attribute for cicadas because they vary so much in shape, size, pattern and colouring, even between species of a single genus. He also noted that in those species lacking timbal covers the opercula were always short and it is only when the timbal covers are well developed does one find elongated opercula.

The relationship between the development of the opercula (structures of metepimeron origin from the thorax) and timbal covers (structures of 2nd abdominal tergum origin) certainly does have an element of truth but it should be noted that Moulton does not claim that the presence of large timbal covers implies elongated opercula and nor is this true. In the present analysis the most elongate opercula occur in clade 22, (character state 38.5), among representatives of the Dundubiini (*Dundubia, Diceropyga* and *Cosmopsaltria*), genera also with large tymbal covers. All other genera with large timbal covers (e.g., the majority of those in clade 21) do not possess elongate opercula. The next longest are found amongst the genera *Cryptotympana, Henicopsaltria, Anapsaltoda, Neopsaltoda* and *Psaltoda* (all in a subclade of clade 21), but their opercula extend only a relatively short distance beyond the tympanal cavity. It is interesting to note that the two genera with the largest timbal covers, *Thopha* and *Arunta*, actually have very small opercula (character state 38.6) because the timbal covers probably fulfil the acoustic function of extended opercula.

Not all opercula of species lacking timbal covers are small, although they do qualify as short in the sense of Moulton. In clade 8, *Aleeta* possesses enlarged rounded opercula (a presumed extreme of 38.4), as does *Birrima* in clade 14 and similarly in some species of *Gymnotympana* in clade 12 (38.7). The opercula of *Plautilla* (clade 6), a genus which also lacks true timbal covers, are also enlarged like those of some *Gymnotympana*.

Opercula development has proceeded both distally and medially; in the early stages of development medial expansion mostly dominates (38.0, 38.1, 38.9) (as in the clades 3, 4), with distal development following as seen in clade 22, the Dundubiini (38.5), and genera such as *Psaltoda, Henicopsaltria, Cyclochila* and others (38.2). Extreme enlargement of opercula is always a derived attribute. However, the cladistic analysis also shows a reversal in opercula development in some clades, that is, a trend towards reduction in size. This is perhaps most evident amongst the Chlorocystini (clade 12), where the opercula of *Chlorocysta, Glaucopsaltria* and *Owra* are considerably reduced compared to those of other Chlorocystini. The Prasiini (clade 10) also include genera with small opercula, especially some species of *Lembeja*. Other notable species with exceptionally small opercula are *Cicadetta forresti* (clade 17) and *Pauropsalta nodicosta* (clade 16) within the Cicadettini, and *Taphura* (clade 8), the type genus of the Taphurini. All these genera have other apomorphies suggesting they are highly derived taxa.

Male timbal covers. The possession of timbal covers (character states 44.1, 44.2) is shared by all species of clade 4, representatives of genera occurring not only throughout Australasia but also through all other faunal regions. Timbal cover development is minimal at lower nodes which includes the Australian genera *Parnkalla, Jassopsaltria* and *Tamasa*. Genera more highly derived show a corresponding enlargement of the timbal covers, with genera grouped by upper nodes such as *Psaltoda* (Australia), *Lyristes* (Palaearctic), *Arunta* and *Thopha* (Australia) and *Platypleura* (Africa and Asia) possessing the largest timbal covers and which may have reached the maximum physical size possible; any more forward development would encroach upon wing mobility in these genera while in *Arunta* and *Thopha* (45.1) further outward rounding of the timbal covers would appear to be limited by the wings at rest. The timbal covers of clade 20, representing the tribes Cicadini and Dundubiini of mainly Indo-Australian and western Palaearctic origin, lack complete ventral development (47.1) and appear to have followed a different line from genera comprising clade 21 (Australasian, Afrotropical, Palaearctic and Nearctic genera).

The timbal covers of clade 6, representing a group of Neotropical genera, also have seemingly derived independently from other genera of clade 4. These Neotropical genera have two notable features relating to their timbal covers; (a) they are substantially reduced along the dorsal margin leaving the upper half of the timbals exposed (46.1), and (b) the metanotum is lobed creating "covers" that project posteriorly from the thorax to partly cover the upper half of the timbals left exposed by the anteriorly projecting abdominal timbal covers (14.1). These metanotal timbal covers are most developed in *Plautilla* where they appear to entirely replace the function of the abdominal timbal covers. Further, within clade 5, (the sister group of clade 4), where all genera lack timbal covers, clades 8 and 9 show trends in the shape of the timbal cavity margin. In clade 8 the genera *Aleeta* and *Tryella* have a cavity margin slightly ridged, suggesting the initial development of what may be a timbal cover. Clade 9, however, shows an opposite trend in that some members of the Chlorocystini (clade 12, a subclade of 9) possess an extreme rounding off of the cavity margin. A similar rounding of the timbal cavity margin is also evident in part of clade 17, where species such as *Pauropsalta eyrei, P. basalis* and *Cicadetta minima* have a cavity margin that is clearly more rounded than in allied genera.

Nowhere does the analysis suggest that timbal covers arose, were lost and then developed again, a trend that must be considered highly unlikely.

Timbals. There are marked differences between the comparatively small timbals of the Tettigarctidae (clade 1) which occur in both males and females (character state 104.0) and the large timbals found only in males of the Cicadidae (clade 2). They function differently, those of Tettigarctidae are used to create substrate-borne vibrations (Claridge *et al*., 1999), while those of the Cicadidae produce air-borne calls. The acoustic system of the Tettigarctidae corresponds to that of the Cercopoidea (outgroup) and their allies, but the highly efficient timbal mechanism and associated resonant abdominal cavity of the Cicadidae are unique to this family. Thus, the small timbals of Tettigarctidae must be considered plesiomorphic while those of the

Cicadidae are apomorphic. In other words the small, less functional timbals of Tettigarctidae are not vestigial as believed by Boulard (1998) but rather have never attained the development exhibited by the Cicadidae. On the other hand, the cladistic analysis confirms that the apparent absence of timbals in *Platypedia* (clade 3) is due to a loss of these structures as previously suggested (Boulard, 1986a, 1988a). Further, the small and substantially ineffective timbals of *Froggattoides* and *Pauropsalta nodicosta* (clade 16) are an apomorphic condition rather than plesiomorphic, that is, they have lost their effectiveness, no doubt due to the development of supplementary wing-clicking mechanisms as an alternative means of communication.

The timbals of the Cicadidae are strongly ribbed and there is a clear progression in the complexity of this ribbing from just a few ribs, in association with a large basal dome, to many ribs with a small basal dome (character 48). Three separate monophyletic groupings independently show this trend, the Indo-Australian Prasiini/Chlorocystini plus Taphurini (clade 7), in *Tibicina haematodes, Tettigades ulnaria* and *Platypedia putnami* (clade 3) and in *Cicadetta forresti* of the Cicadettini (clade 17). Such timbal development has occurred only in association with exposed timbals and timbal development within the larger cicadas, such as Cyclochilini, Thophini, Platypleurini and Cryptotympanini (clade 21). Possession of large timbal covers has, if anything, developed less complexity (i.e. loss of ribs).

The analysis shows no example of timbal loss (or near loss) followed by redevelopment of timbal complexity.

Stridulatory mechanisms. Boulard (1976a) emphasized the significance of stridulatory mechanisms in defining family-group taxa and originally based his family and subfamily classification largely upon such mechanisms. However, later he conceded that these mechanisms did not always imply such relationships and he abandoned much of this emphasis (Boulard, 1976b, 1986b). Stridulatory mechanisms in cicadas were noted by Boulard (1986b) to fall within three, or possibly four, broad categories.

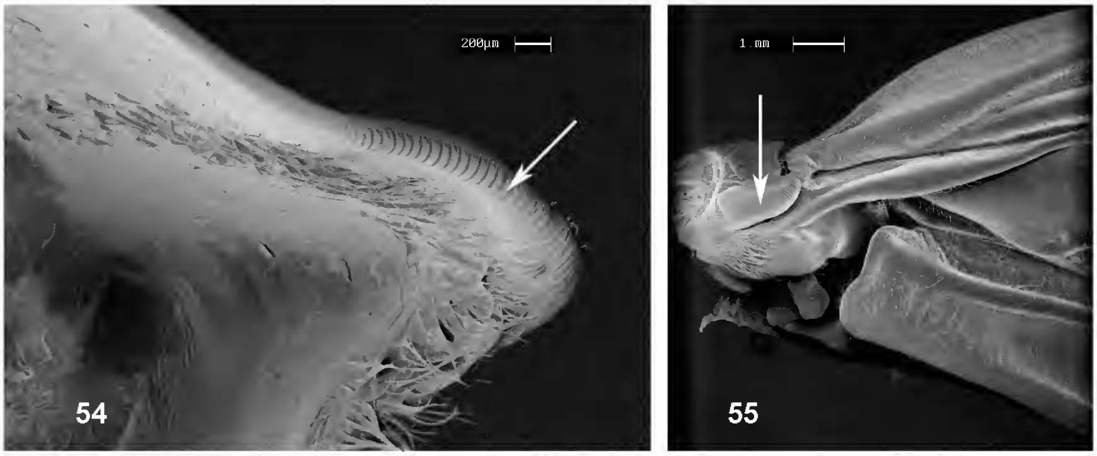
Boulard (1976a, 1996c) records the presence of a mesonotal file on the anterior angles (plus fore wing plectrum) in *Tettigades, Calliopsida, Babras, Subpsaltria, Tibicina* (in *T. quadrisignata* Hagen and *T. nigronervosa* Fieber these files are less prominent and in *T. haematodes* they are just discernible), *Clidophleps, Zammara* (absent in *Z. columbia*), *Onoralna, Plautilla* and in some *Chonosia* (character state 10.1). The cladistic analysis suggests that some of these genera are closely allied (e.g., *Tibicina* with *Tettigades, Plautilla* with *Odopoea* and *Zammara*); these are confined within two distinct clades, the members of each of these clades possessing mesonotal files except for *Platypedia* and *Odopoea* (clades 3 and 6).

Two further stridulatory systems identified by Boulard are found in the genera *Maroboduus* (= *Ydiella*) and *Moana*. In *Maroboduus* interaction between the costa of the hind wing and last anal vein of the fore wing produces sound, and in *Moana* sound production originates from interaction between a file on the flange of the mesothoracic scutellum and the fore wing. As both are confined to single genera these mechanisms do not contribute to resolving phylogenetic relationships at higher levels.

Boulard (1986b) also identified a possible fourth stridulatory system that is associated with the male genitalia of *Carineta*. Sound can be produced manually from the genitalia but has yet to be confirmed as a natural occurrence amongst these cicadas or in allied genera.

A stridulatory system previously unrecorded is found in the Australian genus *Cyclochila* (Figs. 54, 55). Sound is produced by both sexes from the interaction between a file on the underside of the lateral angle of the pronotal collar and a similar scraper on the base of the fore wing but the purpose of the sound remains unknown. Audible sound can be produced from hand held specimens by articulation of the fore wing.

Another means of producing sound is wing flicking, although this appears to have no special associated structures except that in some species the fore wing costa is distinctly angled, which appears to increase the volume of the sound. Wing flicking is usually performed by females in response to male calls but in some species is also performed by males, especially those species with angled fore wing costas. In some situations wing flicking produces little or no sound and in these cases appears to be essentially a visual cue (Cooley, Hill and Marshall, pers. comm.). There are several records for the Cicadettini; in Amphipsalta (I. Myers & J.G. Myers 1924; J.G. Myers, 1929; Fleming, 1969; Dugdale & Fleming, 1969; Fleming, 1973; Lane, 1995; and others), in



Figs. 54–55. *Cyclochila australasiae*: (54) stridulatory file on underside of lateral angles of pronotal collar; (55) stridulatory scraper on fore wing base.

Kikihia (Dugdale & Fleming, 1969; Fleming, 1973; Lane, 1995), in *Maoricicada* (Dugdale & Fleming, 1969; Lane, 1995), in *Notopsalta* (Lane, 1995), in *Rhodopsalta* (Lane, 1995), in *Cicadetta* (Houston & Gwynne, 1986; Gwynne, 1987; Popov, 1981; Gogala & Trilar, 2004), in *Cicadatra* (Boulard, 1992; Gogala & Trilar, 1998, 2003) and in *Pagiphora* (Gogala & Trilar, 2003). Within the Dundubiini wing flicking has been recorded in *Aceropyga* (Duffels, 1988), in the Tibicinini in *Magicicada* (Cooley & Marshall, 2001) and within Chlorocystini in *Cystosoma* (Doolan, 1981), but the phenomenon is even more widespread (Cooley, Marshall & Hill, pers. comm.). Wing flicking in those genera with a mesonotal file as discussed above (e.g., *Tibicina* and *Okanagana*, in addition to *Platypedia* which appears to have lost its file) are excluded here because their wing action appears to be of a different nature. Abnormal angulation of the fore wing costa as seen in genera such as *Froggattoides, Amphipsalta* and undescribed genera represented by *Pauropsalta nodicosta* and *Abricta borealis* and others, is male orientated and may be of a different origin from female wing flicking. Because wing flicking is so widespread amongst females it is a likely synapomorphy for the Cicadidae as a whole, if not the Cicadoidea, but the phenomenon remains insufficiently understood to draw sound conclusions.

Implications for extant families, subfamilies and tribes

The strict consensus tree, in association with jackknife and T-PTP percentages (Fig. 56), supports five primary clades (clades 1–5). These five clades are here considered to represent family and subfamily rankings in a hierarchical classification (Fig. 57). Clades 6–30 are considered to incorporate tribal rankings (Fig. 58). These 25 clades support currently accepted family, subfamily and tribal groupings only in part. The degree of support and deviation is discussed below. A revised family-group classification based upon these findings is then proposed.

On the monophyly of Tettigarctidae

In an earlier work (Moulds, 1990) I listed eight differences between the living Tettigarctidae and living Cicadidae *sensu lato*. While these differences were not identified as apomorphies or plesiomorphies they do highlight the considerable difference between the Tettigarctidae and all other cicadas. These features were previously identified by Evans (1941) and include the following: fore wing venation complete; radial sector (Rs) arising near wing base, and veins 1A and 2A separated; nervous system with thoracic ganglia separated, the abdominal ganglia fused with the third thoracic; male genitalia with styles; tarsal empodia present; auditory tympana absent; timbals present in both sexes; male abdomen without a resonant chamber; pronotum greatly expanded concealing much of mesonotum.

The very distinct nature of the Tettigarctidae, including both extant and fossil genera, has attained universal acceptance as a monophyletic group at family rank (e.g., Evans, 1941, 1963; Kato, 1954, 1956; Boulard, 1976a, 1998; Boulard & Nel, 1990; Duffels, 1993; Hayashi, 1984; Chou *et al.*, 1997; Shcherbakov, in prep.).

The cladistic analysis has shown that the monophyly of Tettigarctidae (clade 1, Fig. 59), based upon the only two known extant species, is very strongly supported by 14 autapomorphies (characters 36, 65, 67, 107–117), a jackknife support of 100%, and a T-PTP of 0.01%. Some of the character attributes may in fact be apomorphic for the genus *Tettigarcta* only, rather than at family level, but a lack of fossil evidence makes interpretation somewhat inconclusive. Nevertheless, there are so many apomorphies here that the monophyly of the Tettigarctidae is not in dispute.

Further, three attributes of *Tettigarcta* suggest that this genus may be highly derived, representing the end of a lineage that has otherwise become extinct. The derived status of the narrow head amongst the Tettigarctidae has been previously discussed. The prostrate fore leg primary spine always occurs as a derived state elsewhere in the Cicadoidea and there is no reason to doubt that it is also apomorphic for *Tettigarcta*. The narrow wing margin of *Tettigarcta* may also be a derived condition, not because the margin has narrowed as in some derived Cicadidae, but because early tettigarctids completely lacked a developed wing margin.

On the monophyly and sister group of Cicadidae

In documenting the Tettigarctidae (Moulds, 1990) I also suggested that all other cicadas apart from Tettigarctidae formed a monophyletic group, the Cicadidae. The following synapomorphies were listed: fore wing vein R+Sc arising from node; fore wing veins 2A+3A concurrent for most of their length; auditory tympana present and male abdomen substantially cavernous forming a resonant chamber. Hayashi (1984) also listed as features of the Cicadidae the presence of auditory tympana, plus a capsule-like male pygofer and the modification of the male 10th abdominal segment into a hook-like uncus. Chou *et al.* (1997) identified six synapomorphies in their cladistic analyses; the presence of opercula, auditory organ present, pronotum shorter than mesonotum, fore wing veins CuP and 1A fused, distance between eyes greater than diameter of eyes and uncus present; the last should be excluded as both Tettigarctidae and Cicadidae have an uncus while the second last has many exceptions.

I also proposed that the Tettigarctidae form a sister group to all other cicadas (Moulds, 1990), an idea first mooted by Bekker-Migdisova (1949) and Evans (1957) and more recently proposed by Hayashi (1984) and subsequently considered plausible by Duffels (1993) and Boulard (1998).

The cladistical analysis clearly supports these views. The clade forming the sister group of the family Tettigarctidae (clade 2, Fig. 59) should also logically represent a family group taxon. The exceptional support for this clade, which includes 17 non-homoplasious apomorphies, (characters 44, 57, 63, 71, 94–106, a jackknife support of 100%, and a T-PTP of 0.01%), leaves little argument for accepting additional families within the Cicadoidea by dividing the Cicadidae. Thus, the Cicadoidea are here considered to represent just two families, the Tettigarctidae and Cicadidae, confirming currently accepted views.

On the monophyly of the subfamily Cicadinae

The group of cicadas possessing abdominal timbal covers (here considered the subfamily Cicadinae) has been widely accepted as a monophyletic group ever since Distant (1906b) laid down the basic system of cicada classification based upon these structures. There is disagreement only in so far as some authors recognize these cicadas as two groups, those with either incomplete or complete covering of the timbal cavity, subfamilies Cicadinae and Platypleurinae (= Tibiceninae) respectively.

Kato (1954), Duffels (1993) and others have questioned this classification that is based only on a single male character and which leaves females unclassifiable. Despite these shortcomings no alternative classification has been proposed. However, more recently, Hayashi (1984) has identified a second character for these cicadas with timbal covers, a very short and linear metanotum, entirely concealed under the mesonotal cruciform elevation, a character present in both sexes. The discovery of this second character notably increases the likelihood of the Cicadinae being a truly monophyletic group. Further, Singh-Pruthi (1925) found broad similarities in the male genitalia of the Cicadinae and believed he could differentiate the Cicadinae from the Tibicininae but his characters are too vague for critical analyses.

The division of the Cicadinae into Cicadinae and Platypleurinae based on complete or incomplete covering of the timbal cavity has been questioned by Moulton (1923), Kato (1932, 1954), Duffels (1993) and others. Considerable difficulties arise in interpreting the degree of cover in genera such as *Platypleura* where development of the timbal cover does not quite extend sufficiently to completely close the timbal cavity. Further, apparently closely related genera are attributed to different subfamilies under this arrangement (Moulton, 1923; Wagner, 1960, 1964; Duffels & van der Laan, 1985; Duffels, 1991, 1993). It would seem there is little doubt that these groupings are not monophyletic although some authors retain this classification.

Clade 4 (Fig. 57) is here interpreted as representing the Cicadinae. Justification for the Cicadinae based upon the traditional interpretation of possessing timbal covers is supported as a monophyletic group (Fig. 59, character state 44.2). The Cicadinae are further supported as a monophyletic group by one other non-homoplasy (character 50), development of the distal shoulder of the male pygofer. Jackknife support is relatively low at 65% but the T-PTP score shows strong support at 0.01%. The monophyly of the Cicadinae is also supported by two other homoplasious character states, 24.1 and 38.0.

Notable new inclusions in the Cicadinae are the Australian genera *Parnkalla, Jassopsaltria* and *Burbunga* and the South American genus *Plautilla*. The inclusion of *Plautilla* with the Cicadinae is discussed below under the heading "On *Plautilla* and the Plautillinae".

Partial development of the timbal covers, the character used previously to divide the Cicadinae into a second subfamily, the Platypleurinae, is not borne out by this analysis. Partial development of the timbal covers is a plesiomorphic condition of several lineages within the subfamily as discussed above under the heading "Some notable character trends".

On the monophyly of the subfamily Tibicininae

The other major lineage previously recognized within the Cicadidae is the subfamily Tibicininae. Liu (1978: 146) commented on the belief that the Tibicininae are "nothing but a dumping ground for a miscellany of unrelated forms characterized by a single negative quality". That plesiomorphic feature is the absence of timbal covers. Boulard (1976a) draws attention to the problem within *Orapa* Distant, from East Africa, which includes *O. elliotti* (Distant) which possesses timbal covers as well as *O. lateritia* Jacobi (an undisputed *Orapa* species) which lacks timbal covers. The monophyly of the Tibicininae therefore has been considered doubtful, or at very least required substantiating.

In the cladistic analysis the Tibicininae are considered to be represented by clade 5 (Fig. 57). Despite being defined previously by a single negative "attribute", lack of timbal covers, the group is in fact much better supported. Eight apomorphies, including three that are non-homoplasious states (61.1, 63.2, 68.2), are identified (Fig. 59) together with a reasonable jackknife support of 80%, and a strong T-PTP score of 0.01%.

There is, however, one very notable exclusion from the subfamily, the genus *Tibicina* which is placed basally on the tree, in clade 3. As this genus is the type genus for the subfamily, then the Tibicininae as currently known, must take a new name. Other exclusions are the Australian genera *Parnkalla, Jassopsaltria* and *Burbunga* which have been moved to the Cicadinae as mentioned above. There are no new inclusions from outside the Tibicininae.

On the sister group of Tettigadidae/Tettigadinae and Platypediinae

Kato (1956) placed the Tettigadidae as the sister group of the Cicadinae + Tibicininae, with the Tettigarctidae and Platypediini as successive sister groups, but the arrangement was not substantiated. Chou *et al.* (1997) obtained a similar sister group relationship for Tettigadidae from their cladistic analyses, supporting the monophyly of Tettigadidae + Cicadinae + Tibicininae by the presence of timbals and the ability to make loud noise, while the Cicadinae + Tibicininae were supported in having a subgenital plate (more correctly termed sternite VIII) that is not long or slender. However, I have previously commented on some of the shortfalls of Chou *et al.* which leaves the sister group relationship of the Tettigadidae still largely unsubstantiated.

Boulard (1988a: 64) stated that Platypediini, forming the subfamily Platypediinae, is the neighbouring tribe to the Tibicinini. On the other hand, Kato (1956) suggested that *Platypedia* and *Neoplatypedia* are the sister group to all other cicadas (excluding Tettigarctidae) as the family Platypediidae. However, neither Boulard nor Kato provided reasons for their conclusions.

Chou *et al.* (1997) concluded that the Platypediini (considered by them to be at subfamily rank) were allied to the Tettigadinae, Tibicininae and Cicadinae, based on two somewhat dubious apomorphies, namely a large abdomen and a pronotal anterior margin more slender than the posterior margin. Heath (1978) also recognized the relationship between the Platypediinae and the North American allies of *Tibicina* (i.e. *Okanagana, Tibicinoides* and *Clidophleps*) suggesting they be placed at a tribal ranking within the Tibicininae. Later (Heath, 1999) proposed subfamily rank for the group.

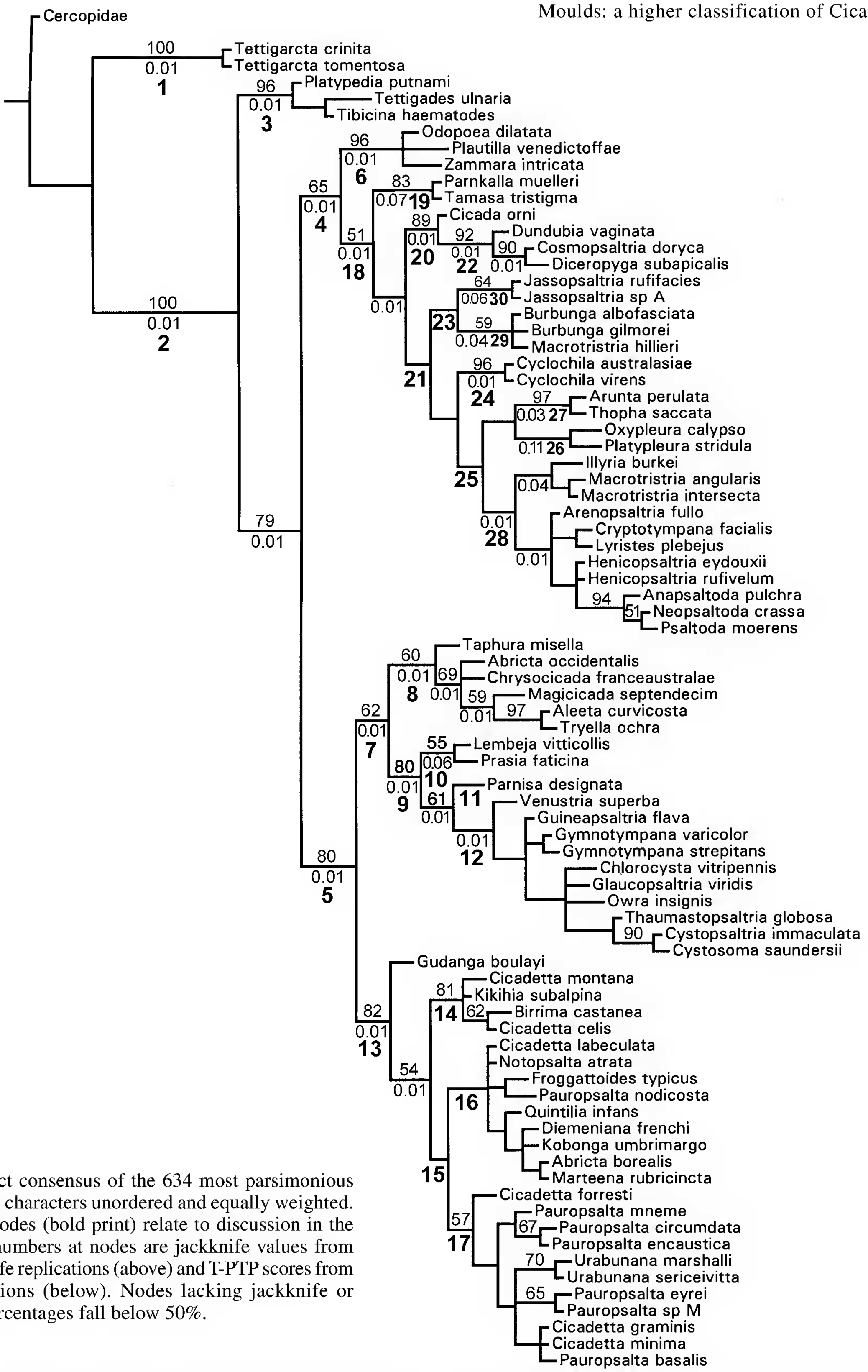


Fig. 56. Strict consensus of the 634 most parsimonious trees with all characters unordered and equally weighted. Numbered nodes (bold print) relate to discussion in the text. Other numbers at nodes are jackknife values from 1000 jackknife replications (above) and T-PTP scores from 100 replications (below). Nodes lacking jackknife or bootstrap percentages fall below 50%.

While the separation of the Tettigadinae and Platypediinae from other cicadas is largely maintained in the cladistic analysis, they fail to retain their individual subfamily rankings. Together with *Tibicina* they are here considered to form a new subfamily concept (clade 3, Fig. 57) comprising the Tettigadinae + Platypediinae + *Tibicina* and its allies (which currently form the tribe Tibicinini excluding *Magicicada*, see Taphurini below). This monophyly is well supported by six apomorphies, including three non-homoplasious states (Fig. 59), a jackknife of 96% and a strong T-PTP score of 0.01%.

Significantly this subfamily group forms a sister group to all other Cicadidae. This carries important implications for biogeography and the development of subsequent phylogenetic studies. Kato (1956) had previously recognized the distinctive nature of the Tettigadinae and Platypediinae but he overlooked *Tibicina* placing it as a highly derived Tibicininae.

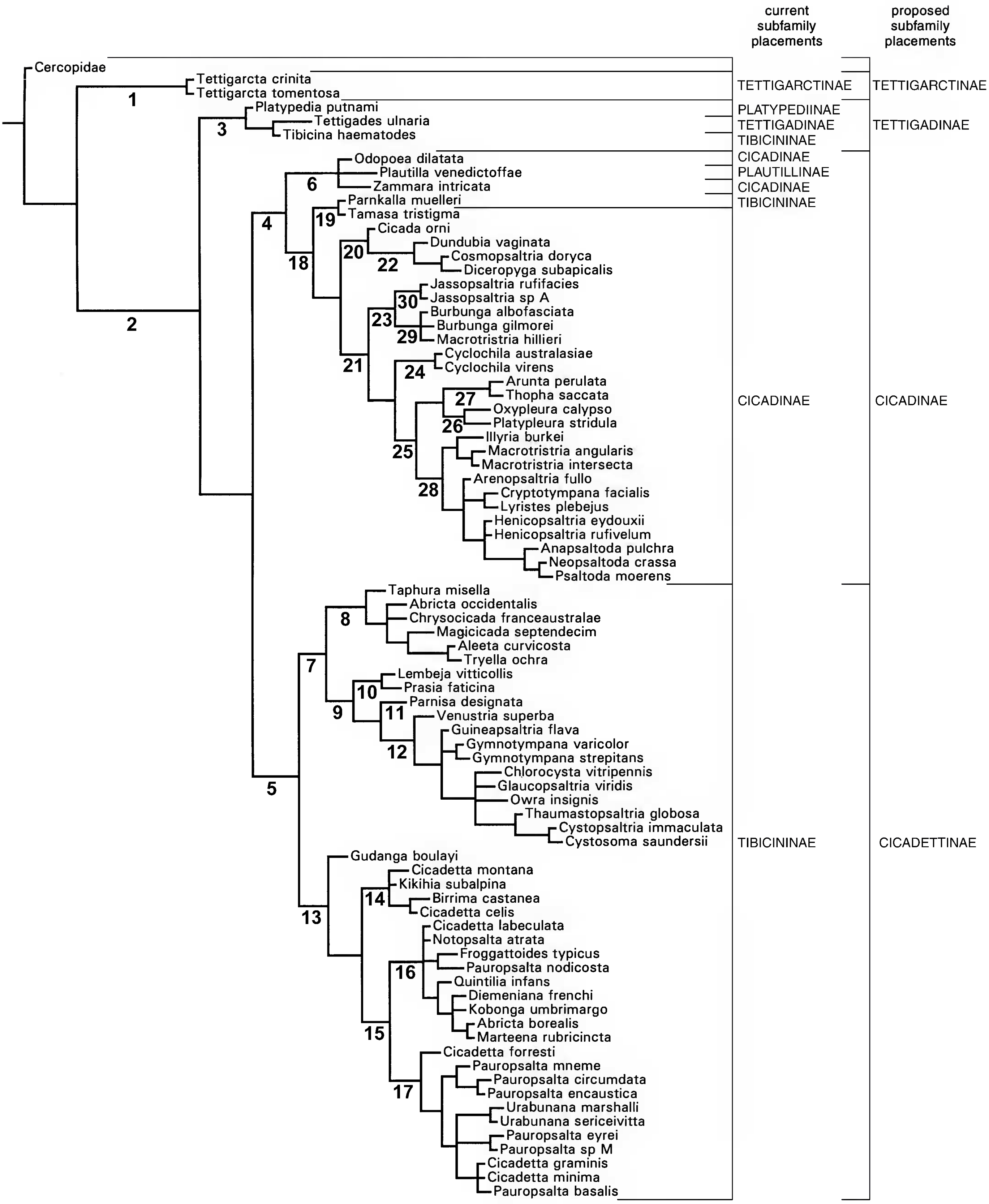


Fig. 57. Strict consensus tree showing current subfamily placements for genera, together with their proposed subfamily placements under the revised classification derived from this study. Numbered nodes are those referred to in the text.

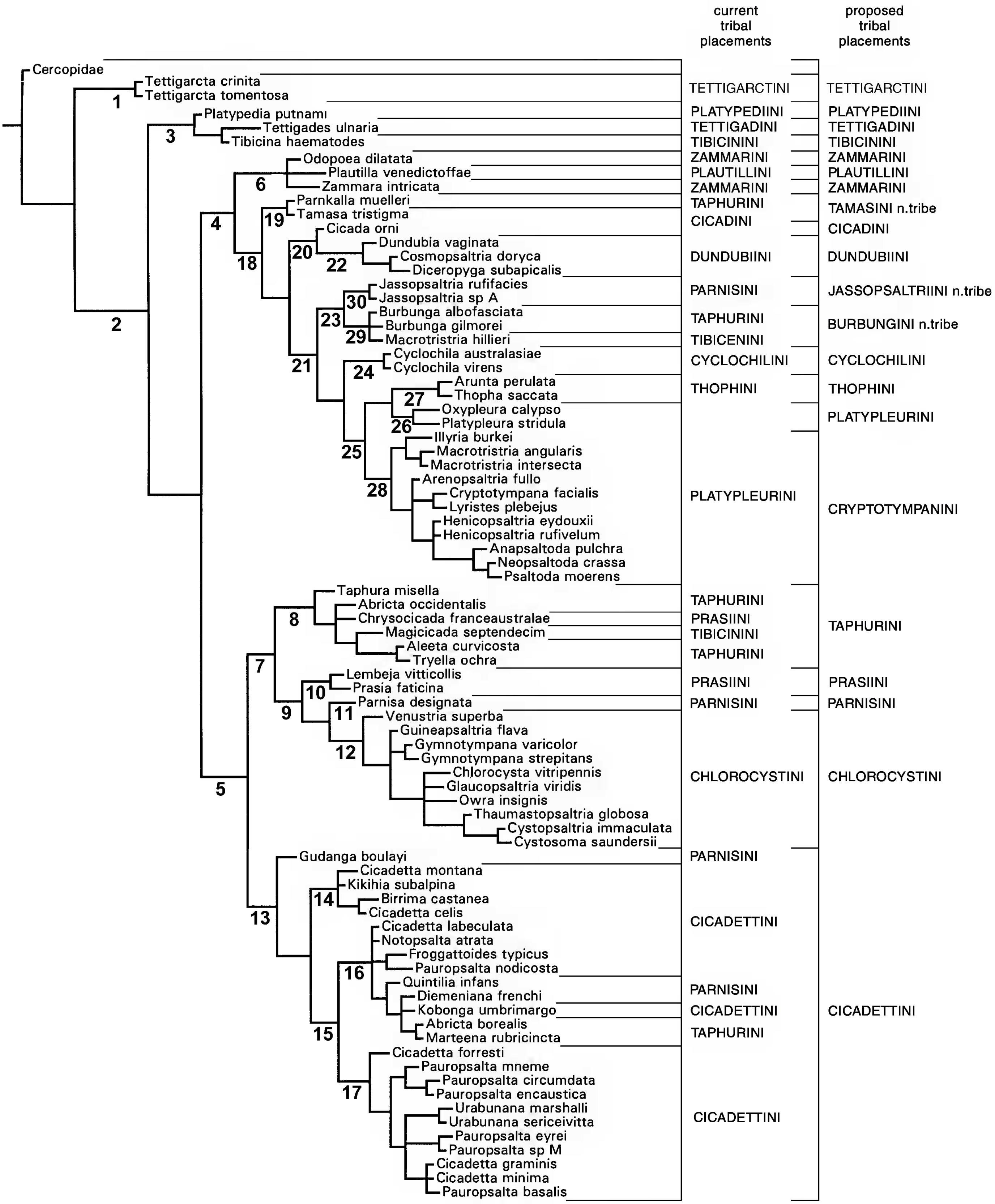


Fig. 58. Strict consensus tree showing current tribal placements for genera, together with their proposed tribal placements under the revised classifications derived from this study. Numbered nodes are those referred to in the text.

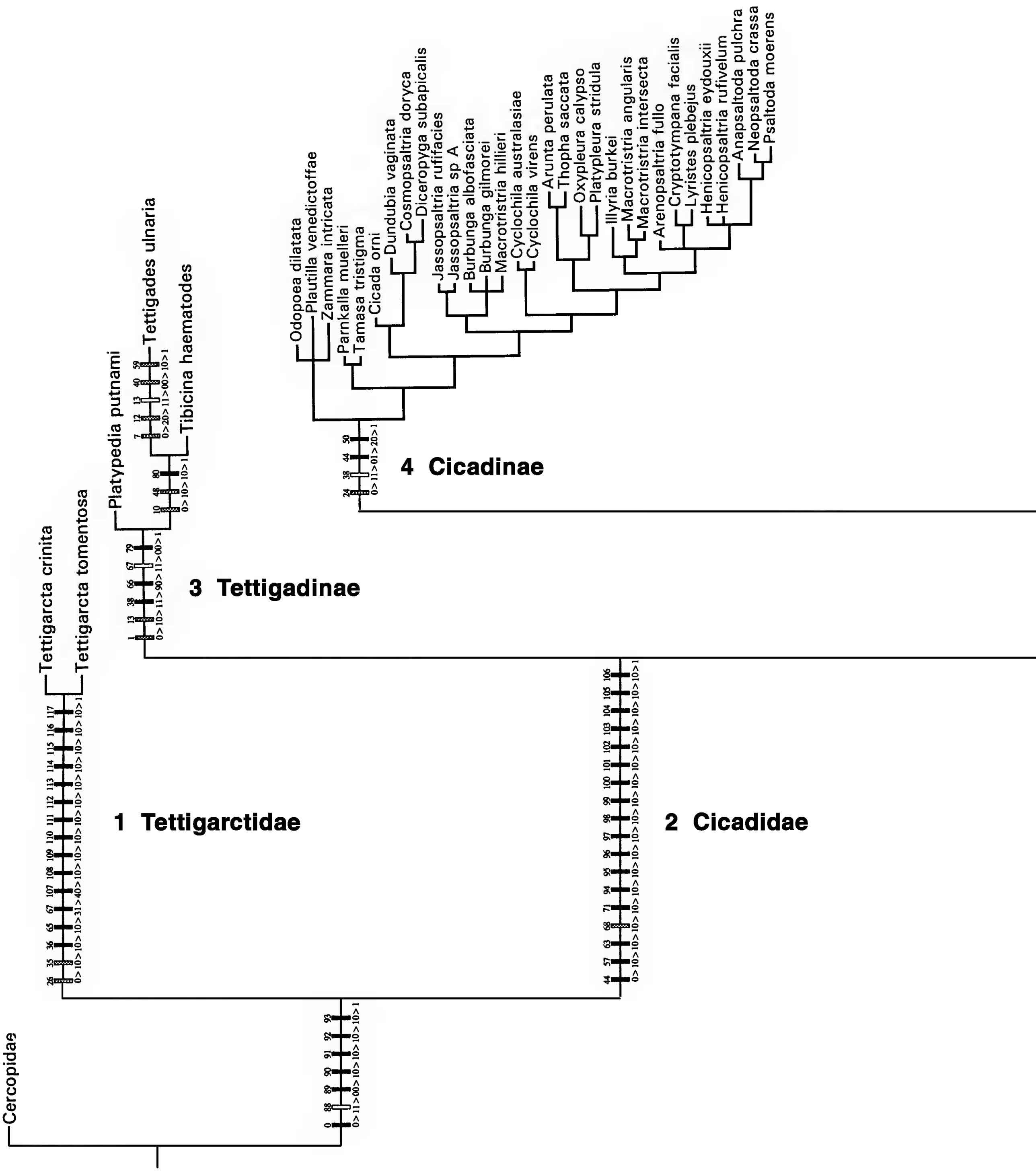
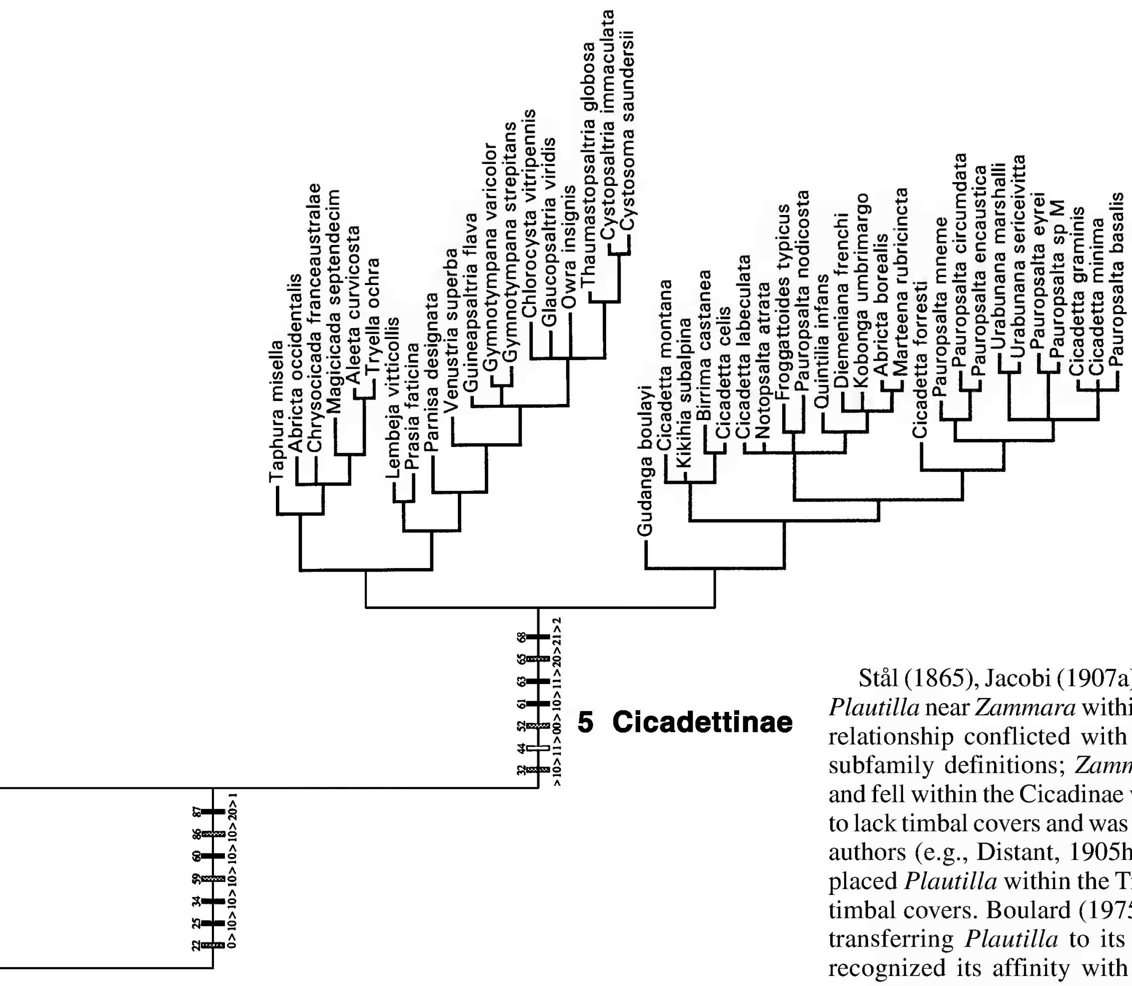


Fig. 59 (continued on facing page). One of the 634 most parsimonious trees showing names of transformations for basal nodes. These nodes and characters transformations are identical for all 634 trees. Numbered nodes relate to discussion in the text. Proposed families and subfamilies are named at their respective nodes. Black bars = non-homoplasious forward change; grey bars = homoplasious forward change; white bars = reversal (whether homoplasious or not). Numbered nodes refer to discussion in text.



On *Plautilla* and the Plautillinae

Boulard (1975a) discussed the distinctive features of the South American genus *Plautilla*, the metathoracic lobes that act as timbal covers, narrow anal lobes to the hind wings, a narrow head, broad paranota, pronounced narrowing of the body at the junction of the thorax and abdomen, membranization of sternites III–VI, large dish-like male opercula extending lateroventrally, the short broad ulnar cells of the fore wings and the presence of a thoracic stridulatory mechanism. Most of these features can be identified as highly derived attributes.

Distant (1905h: 563) placed *Plautilla* between the Cicadettini and Hemidictyini. He likened the fore wing venation (presumably meaning the closeness of veins M and CuA) to that of the Cicadettini, and its narrow head to that of the Hemidictyini.

Stål (1865) remarked on the similarity of *Plautilla* to *Zammara*, an association discussed at some length by Boulard (1975a). Boulard (1976a: 403) also considered *Plautilla* to be very distant from *Tettigades* and *Clidophleps*. Further, Boulard (1994) has commented on the remarkable similarity of the membranous abdominal sternites of *Plautilla* to those of *Zouga* Distant from Morocco although, as Boulard points out, *Zouga* is clearly unrelated in other characters and is currently placed within the tribe Parnisini of the Tibicininae. Hayashi (1984) strongly believed that *Plautilla* falls within the Cicadidae based upon male genitalic characters.

Stål (1865), Jacobi (1907a) and Handlirsch (1925) placed *Plautilla* near *Zammara* within the Cicadinae. However, this relationship conflicted with entrenched views on family/subfamily definitions; *Zammara* possessed timbal covers and fell within the Cicadinae while *Plautilla* was considered to lack timbal covers and was excluded. Consequently, some authors (e.g., Distant, 1905h, 1906b; Metcalf, 1963) have placed *Plautilla* within the Tibicininae, cicadas that lacked timbal covers. Boulard (1975a) addressed this problem by transferring *Plautilla* to its own family but nevertheless recognized its affinity with *Zammara* by suggesting the origin of *Plautilla* was close to the members of *Zammara*, an association confirmed here by the cladistic analysis. *Plautilla* does, in fact, possess timbal covers, present as well-developed ridges but they lack the typical anterior expansion of most timbal covers.

The cladistic analysis clearly places *Plautilla* with the two South American genera, *Zammara* and *Odopoea* (clade 6, Fig. 60), which together form a clade that is the sister group to all other Cicadinae (clade 18). The monophyly of *Plautilla, Zammara* and *Odopoea* is well supported by eight apomorphies, including three non-homoplasious states (Fig. 60), a jackknife of 96% and a strong T-PTP score of 0.01%.

The placement of *Plautilla* in the cladistic analysis with species of the tribe Zammarini (*Zammara* and *Odopoea*) brings into question the status of *Plautilla* at subfamily rank as recognized in current literature. If *Plautilla* is considered at subfamily rank then the Zammarini, as the sister group to *Plautilla*, should also be given subfamily rank. However, the Zammarini clearly do not deserve subfamily rank and the situation is best overcome by placing *Plautilla* at tribal rank. This then, raises the question of the status of clade 6, comprising Plautillini and Zammarini. It could be argued that this is the clade that deserves subfamily rank as it is well supported by apomorphies. While there is some justification for placing this clade at subfamily rank I prefer to take a conservative approach at this time by including *Plautilla* (as the Plautillini) and the Zammarini, as part of the Cicadinae defined in the analysis by clade 4 (Fig. 57). Future studies in molecular phylogeny of the Cicadoidea may help clarify this situation.

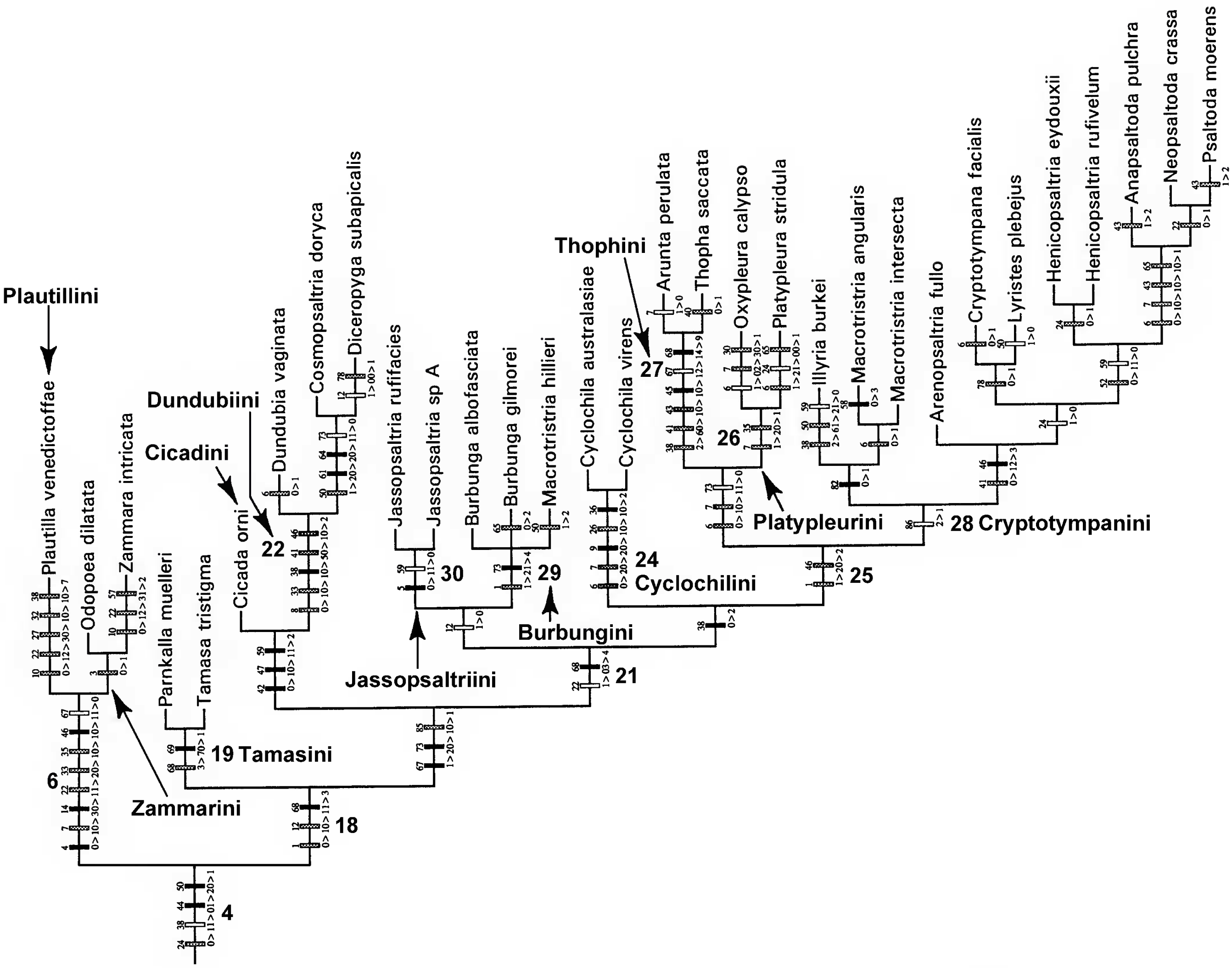


Fig. 60. Character transformations within clade 4 of the same tree shown in Fig. 59. Numbered nodes relate to discussion in the text. Note that resolution within this clade differs little from the strict consensus tree shown in Fig. 56. Tribal groupings are those proposed under this study. Black bars = non-homoplasious forward change; grey bars = homoplasious forward change; white bars = reversal (whether homoplasious or not).

On the monophyly of the Chlorocystini

Boer (1995b, 1997) identified a single apomorphy for the Chlorocystini, the S-shaped aedeagus with winged lateral crests. The monophyly of the group is supported by the cladistic analysis presented here (clade 12, Fig. 58). Three additional apomorphies have been identified for the suite of taxa used in the present analysis to represent the Chlorocystini (characters 23, 40 and 68, clade 12, Fig. 61); all were used by Boer (1995b) but were found not to support monophyly of the tribe as a whole when an exhaustive range of taxa was used.

Groupings within the Chlorocystini are equivalent to those resolved by Boer (1997) even though characters and/or attributes used are not consistently equivalent. Thus, there is no reason to question any of the phylogenetic conclusions from the far more extensive study of the group by Boer (1995b, 1997) and readers should consult his work for analyses of ingroup relationships.

The genus *Parnisa* falls as the sister group to the Chlorocystini (for discussion see Parnisini below).

On the monophyly of Cicadettini

The Cicadettini have been traditionally defined on a single apomorphy, the fusion or near fusion of the stems of fore wing veins M and CuA; in those species where fusion is incomplete these veins are in part concurrent and arise from the basal cell at a common point (Kato, 1956, 1961; Liu, 1978; Boulard, 1996a).

For the most part this definition appears satisfactory but it also introduces elements of uncertainty and doubt. Significantly, *Cicadetta montana*, the type species of *Cicadetta*, which in turn is the type genus of the Cicadettini, has veins M and CuA just meeting at the basal cell and doubtfully concurrent at all. Similar situations can be found in genera of allied tribes, e.g., *Cystosoma* and *Venustria* (both tribe Chlorocystini) and *Ueana* (tribe Taphurini), as well as in genera considered quite distant from Cicadettini, e.g., *Zammara* (tribe Zammarini) and *Moana* (tribe Dundubiini). Conversely, some individuals of genera otherwise clearly falling within the Cicadettini have veins M and CuA entirely separated, e.g., some individuals of

Kobonga froggatti, K. umbrimargo, Pauropsalta extrema and *Cicadetta torrida*. Thus, the Cicadettini may not be entirely monophyletic or may even be largely polyphyletic; either way the tribe requires redefining.

The cladistic analysis shows that the fusion of fore wing veins M and CuA does not define a monophyletic group. I here reinterpret the tribe Cicadettini as comprising clade 13 (Fig. 58), a group encompassing the genera previously included in the Cicadettini plus genera that previously fell outside the tribal definition. This new concept for the Cicadettini is well supported by three apomorphies, including two non-homoplasious states (clade 13, Fig. 62), a jackknife of 82% and a strong T-PTP score of 0.01%. It is a far broader concept in that it now not only encompasses all those genera previously included, but adds those genera with fore wing veins M and CuA separate that otherwise have a trifid male aedeagus.

Genera previously excluded from the Cicadettini, but now falling within the new concept, are *Gudanga* and *Diemeniana* from the Parnisini and *Marteena* from the Taphurini. Two undescribed genera represented by two species previously excluded, *Quintilia infans* and *Abricta borealis*, also now come within the Cicadettini.

On the monophyly of Cryptotympanini, Platypleurini and Thophini

The cladistic analysis supports the current concept of the Cryptotympanini but includes also the genera *Arenopsaltria* and *Henicopsaltria* currently placed in Cyclochilini plus *Illyria* currently in Cicadini (clade 28, Fig. 58). However, the group is poorly supported by just a single homoplasious reversal (Fig. 60, character state 86.1), short accessory glands to the female common oviduct, and a jackknife below 50%, but nevertheless strongly supported by a T-PTP score of 0.01%. An alternative approach would be to remove *Illyria* and *Macrotristria* into an additional tribe, each tribe then based upon a synapomorphy.

These results contrast with suggestions of Boulard (1998: 117) that the Cryptotympanini are a subtribe of the Platypleurini. If that approach were taken then the Thophini would also fall as a subtribe of the Platypleurini.

Of the alternatives mentioned above I prefer to retain the Platypleurini, Thophini and Cryptotympanini as separate tribes (clades 26, 27 and 28 respectively, Fig. 60). I am reluctant to introduce a new tribe for *Illyria* plus *Macrotristria* when the analysis is missing so many genera from this part of the tree. The cladistic support for the Thophini is six apomorphies including two non-homoplasies states, a jackknife of 97%, and T-PTP of 0.03%; the Platypleurini are far less supported by just two homoplasious states, a jackknife below 50%, and a T-PTP of 0.11%; cladistic support for the Cryptotympanini is detailed above.

Future studies in molecular phylogeny may provide a better understanding of the relationships between genera within these tribes.

On the monophyly of the Cyclochilini

The cladistic analysis has highlighted the distinctive nature of the genus *Cyclochila*, as the sister groups of clade 25 (Fig. 60) which incorporates the tribes Thophini, Platypleurini and Cryptotympanini. *Cyclochila* appears not to form a tribal grouping with *Arenopsaltria* and *Henicopsaltria* as previously believed. *Cyclochila* is best considered to be the sole representative of the Cyclochilini. This monotypic tribe possesses five apomorphies, two of which are non-homoplasious. The reduced timbal covers (character state 41.1) and narrower head (1.1) are significant in separating Cyclochilini from node 25 when the developmental trend of these characters is considered (see "Some notable character trends", p. 412). Similarly, the big differences in development of the opercula (character state 3.3), pronotal collar (characters 5, 6) and epimeral lobe (character 10) clearly separated Cyclochilini from Jassopsaltriini and Burbungini. Jackknife support for the node is 96% and T-PTP support is also strong at 0.01%

On the monophyly of the Dundubiini

The Dundubiini are represented in the cladistic analysis by *Dundubia, Diceropyga* and *Cosmopsaltria* (clade 22, Fig. 58). The monophyly is strongly supported by five apomorphies including one non-homoplasious state (clade 22, Fig. 60), a jackknife of 92% and a T-PTP of 0.01%. Similarly, the subtribe Cosmopsaltriina, *sensu* Duffels (1983, 1986, 1993, 1997), here represented by *Diceropyga* and *Cosmopsaltria*, is also well supported by four apomorphies, two of which are non-homoplasious, a jackknife of 90% and a strong T-PTP of 0.01%. Duffels (1993, 1997), Duffels & Turner (2002) and Beuk (2002) have provided cladograms for the genera of the subtribe Cosmopsaltriina and have shown that the presence of lateral processes on the male pygofer can be regarded as a synapomorphy for the species of this subtribe. There is no reason to question the conclusions of Duffels (1993, 1997), Duffels & Turner (2002) and Beuk (2002), based on an extensive study of all species in the Cosmopsaltriina and readers should consult their works for analyses of ingroup relationships.

The sister group of the Dundubiini is identified as the Cicadini (represented by *Cicada*), a point not missed by Kato (1956) in his intuitive phylogeny. The Cicadini + Dundubiini are strongly supported by three non-homoplasious states, a jackknife of 89% and T-PTP of 0.01%. These two tribes in turn form the sister group to the majority of other genera of the subfamily Cicadinae. However, this association is not well supported by the analysis and may be misleading.

Moulton (1923: 78) recognized *Dundubia vaginata* as having advanced attributes (no developed nodal line, fore wings hyaline, "complete" timbal covers and elongate opercula). He did not, however, recognize the significance of the modified male abdomen or reduced hind wing anal lobe as highly derived attributes.

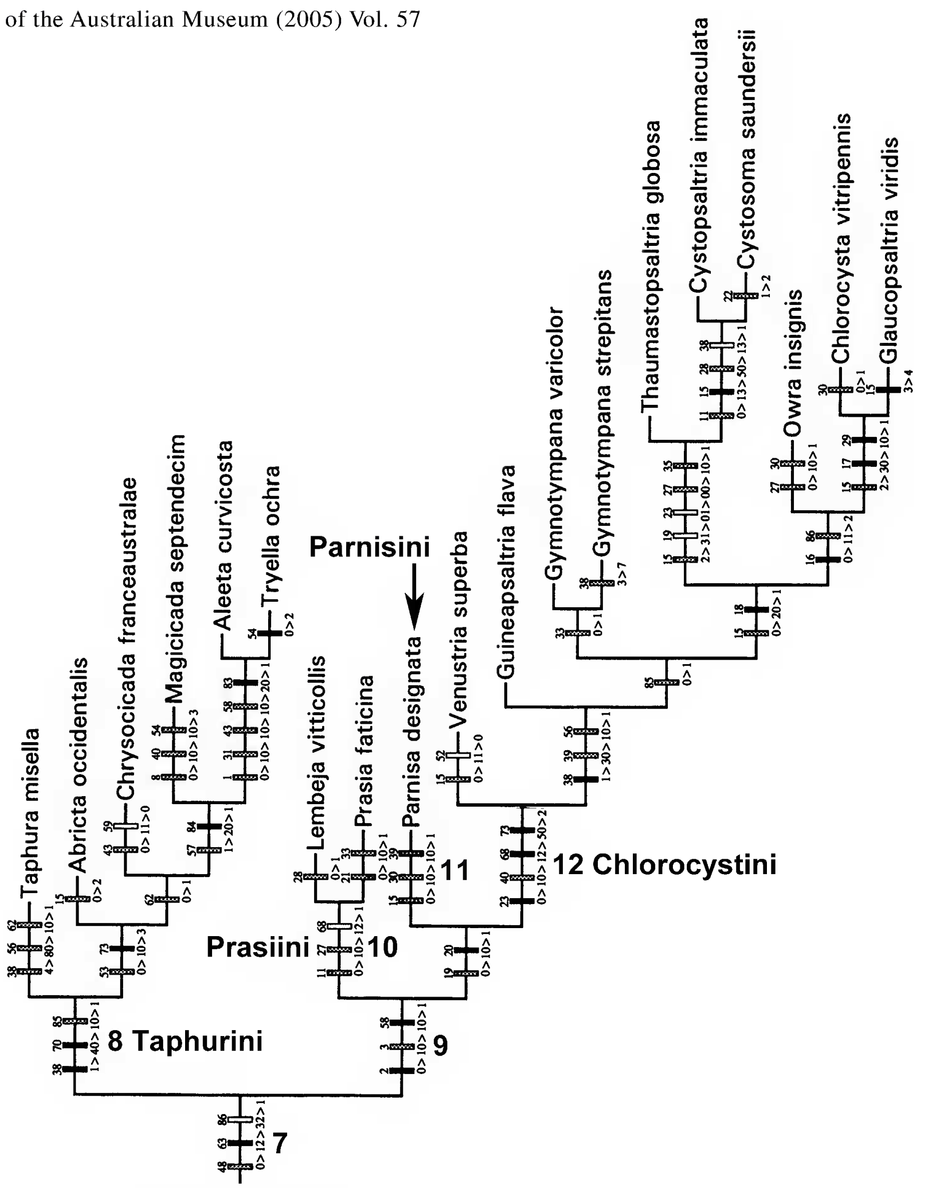


Fig. 61. Character transformations within clade 7 of the same tree shown in Fig. 59. Numbered nodes relate to discussion in the text. Note that resolution within this clade differs little from the strict consensus tree shown in Fig. 56. Tribal groupings are those proposed under this study. Black bars = non-homoplasious forward change; grey bars = homoplasious forward change; white bars = reversal (whether homoplasious or not).

On the monophyly and sister group of Parnisini

The South American genus *Parnisa* was included in the analysis in order to test the monophyly of the Australian genera attributed to the Parnisini, viz. *Diemeniana, Gudanga, Jassopsaltria* and the single Australian representative of *Quintilia, Q. infans*, (which in fact represents an undescribed genus). None of these are monophyletic with *Parnisa* (clade 11, Fig. 56).

Parnisa falls as the sister group of the Chlorocystini, a tribe of mainly New Guinean, Australian and western Pacific distribution. This relationship is supported by two apomorphies including one non-homoplasious state (Fig. 61), a jackknife of 61% and a strong T-PTP score of 0.01%. While this support is reasonable, the next more basal node grouping the Prasiini, *Parnisa* and the Chlorocystini (clade 9), is better supported by three apomorphies including two non-homoplasious states, a jackknife of 80% and a T-PTP score of 0.01%. This implies that Parnisa, at very least, requires serious consideration along with the Prasiini as the sister group of the Chlorocystini. The close relationship of *Parnisa* to the Chlorocystini was unknown to Boer at the time of his phylogenetic studies on the Chlorocystini (Boer, 1995b, 1997, and others) when he chose the Prasiini as outgroup. The close association of *Parnisa* introduces an interesting biogeographic relationship between the South American Parnisini and Australasian Chlorocystini and Prasiini.

On the monophyly of the Prasiini

The Prasiini retain their identity as a tribal group (clade 10, Fig. 61). The monophyly of the tribe is supported by three homoplasious apomorphies, a jackknife of 55% and T-PTP score of 0.06%. They form the sister group to the Parnisini + Chlorocystini. There is no reason to doubt the results of the phylogenetic study of this group by Boer (1995b), which incorporates all genera.

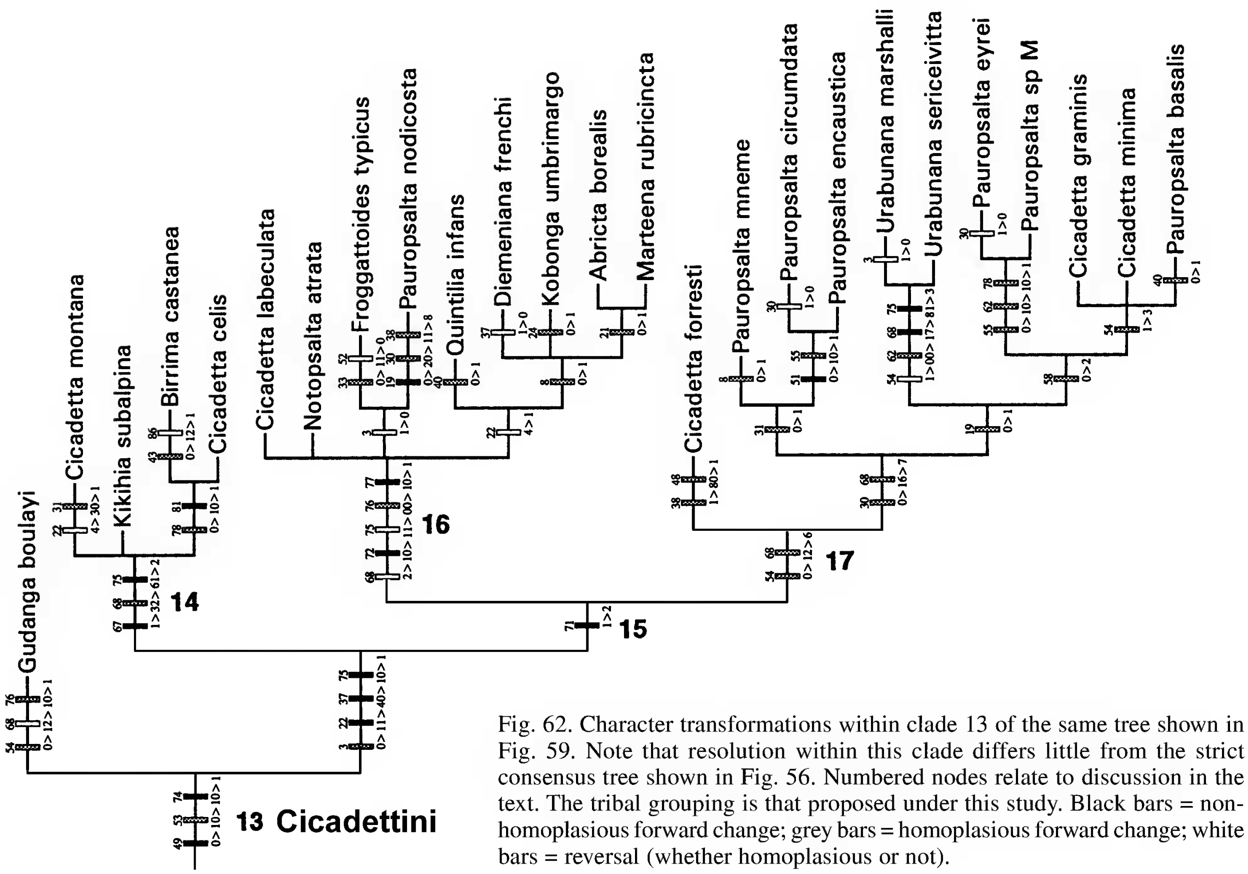


Fig. 62. Character transformations within clade 13 of the same tree shown in Fig. 59. Note that resolution within this clade differs little from the strict consensus tree shown in Fig. 56. Numbered nodes relate to discussion in the text. The tribal grouping is that proposed under this study. Black bars = non-homoplasious forward change; grey bars = homoplasious forward change; white bars = reversal (whether homoplasious or not).

On the monophyly of the Taphurini

The Taphurini are interpreted as clade 8 (Fig. 56) and are supported as a monophyletic group by three apomorphies, including two non-homoplasious states (Fig. 61), a jackknife of 60% and a strong T-PTP of 0.01%. Amongst the genera representing the Taphurini, *Taphura* forms a sister group to all others and the two clades could be interpreted as representing two different tribes. If that view were taken the second clade would become a new tribe supported by two apomorphies including one non-homoplasious character state, a jackknife of 69%, but a strong T-PTP score of 0.01%. A case for two tribes may be justifiable but in the absence of a more extensive analysis incorporating a broad selection of other Taphurini, I err on the side of caution and accept the broader traditional view for the tribe. I do, however, see justification for creating a new subtribe, a case which is discussed in the taxonomic section below.

There is one notable addition to the Taphurini, the periodical cicada genus *Magicicada*. This genus clearly is not allied to the Tibicinini as currently believed but to genera such as *Aleeta* and *Tryella*. Excluded from the Taphurini are *Marteena* to the Cicadettini and *Parnkalla* and *Burbunga* to two new tribes within the subfamily Cicadinae.

New tribal groupings

The cladistic analysis isolates four genera from currently recognized tribal groupings. These fall within two clades within the Cicadinae, one comprising *Tamasa* and *Parnkalla* (clade 19, Fig. 60), the other *Jassopsaltria* and *Burbunga* (clade 23, Fig. 60). These are considered to represent three new tribal groupings formally described in the taxonomic sections below.

Tamasa and *Parnkalla* are united by two apomorphies including one non-homoplasious character state, a jackknife of 83% and a T-PTP score of 0.07% and are here considered to represent the new tribe, Tamasini (Fig. 58).

Jassopsaltria and *Burbunga* are very different from each other in appearance and are here considered to represent two new monotypic tribes, Jassopsaltriini and Burbungini respectively (Fig. 58). The Jassopsaltriini are supported by two apomorphies one of which is non-homoplasious character state, a jackknife of 64% and a T-PTP of 0.06%. The Burbungini are also supported by two apomorphies including one non-homoplasious character state, a jackknife of 59% and a T-PTP of 0.04%.

While none of these supports are strong there are significant character developmental trends supporting the separation of these three tribes. The male timbal covers are reduced (character state 46.0) suggesting they are unlikely to be part of clades 6 or 25 which have large timbal covers, nor do the timbal covers have their lower margin extended vertically before turning anteriorly (character 47) as in clade 29. Also the head lacks lateral elongation of the vertex as in clade 25 (character 1). See discussion of developmental trends of male timbal covers and head width under "Some notable characters trends", p. 412.

TAXONOMY

A revised family classification for the Cicadoidea

As stated earlier, the results of the cladistic analysis provide a convincing argument for dividing the Cicadoidea into just two families, the Tettigarctidae and Cicadidae, an arrangement that had previously attained broad recognition (Fig. 57). In addition, the analysis supports three subfamilies within the Cicadidae; the Cicadinae, Cicadettinae **n.stat.** (= Tibicininae *auct.*) and Tettigadinae. This classification somewhat differs from currently accepted subfamily arrangements in concept and nomenclature. Further, within the Australian fauna, the analysis supports three new tribal groupings in addition to those tribes previously recognized. All these family-group taxa are formally defined below together with a listing of included taxa. Discussion is also included on how these concepts relate to previously held family-group concepts.

Key to the families and subfamilies of Cicadoidea

1 Pronotum greatly expanded and concealing majority of mesonotum .... Tettigarctidae

— Pronotum not expanded over mesonotum, much smaller than mesonotum .... Cicadidae 2

2 Metanotum entirely concealed at dorsal midline .... Cicadinae

— Metanotum partly visible at dorsal midline 3

3 Hind wing veins RP and M fused at their bases; supra-antennal plate usually (but not always) meeting or nearly meeting eye .... Cicadettinae

— Hind wing veins RP and M unfused at their bases; distance between supra-antennal and eye about equal to length of antennal plate .... Tettigadinae

Family Tettigarctidae Distant, 1905

Tettigarctaria Distant, 1905g: 280.
Tettigarctini Handlirsch, 1925: 1161.
Tettigarctinae J.G. Myers, 1928: 391.
Tettigarctines Lameere, 1935: 403.
Tettigarctidae Bekker-Migdisova, 1949: 20–21.

Type genus. *Tettigarcta* White (type species *T. tomentosa* White).

Included subfamilies. Tettigarctinae Distant, Cicadoprosbolinae Bekker-Migdisova.

Diagnosis. Thoracic ganglia separated. Pronotum exceedingly large and concealing majority of mesonotum; paramedian and lateral fissures absent; pronotal collar absent. Mesonotum without a developed cruciform elevation. Fore wing with vein RP arising near wing base; veins 2A and 3A separated for much of their length; nodal line well developed. Hind wing hamulus present. Pretarsal empodia present. Hind coxae overhanging abdomen. Timbals present in males and females. Male abdominal resonant chamber absent. Tympana absent from both sexes. Male sternite VIII not shielding genitalia ventrally. Male genitalia with styles present; pygofer with basal lobe absent; uncus n-shaped in cross-section, apically with sides meeting but not fused; aedeagus with sclerotized subapical dorsal crest. Male reproductive system with testes located anteriorly, centred over abdominal sternites II and III. Female genitalia monotrysian. Female reproductive system with no accessory glands to common oviduct. Nymphs with antennal segments 1 and 2 both very short and together about equal to segment 5; fore femur with a mid-lateral stout spine on outer face; fore tibiae with a large subapical tooth opposing apical tooth; mid and hind tibiae with two stout spines along shank, one each at about ⅓ intervals; hind tibiae with spinal crown including one very dominant flat spine; abdominal spiracles not covered by pleural flaps.

Distinguishing characters. Within the Cicadoidea the following attributes are believed to be unique to Tettigarctidae. Pronotum exceedingly large and concealing most of mesothorax. Fore wing with vein RP arising from node; veins 2A and 3A separated for much of their length; Hind wing hamulus present. Pretarsal empodia present. Male sternite VIII not shielding genitalia ventrally. Pygofer with basal lobe absent. Male reproductive system with testes located anteriorly, centred over abdominal sternites II and III. Female reproductive system with no accessory glands to common oviduct. Nymphs with antennal segments 1 (scape) and 2 (pedicel) both very short and together about equal to segment 5 (3rd flagellomere); fore femur with a mid-lateral stout spine on outer face; fore tibiae with a large subapical tooth opposing apical tooth; mid and hind tibiae with two stout spines along shank, one each at about ⅓ intervals; hind tibiae with spinal crown including one very dominant flat spine; abdominal spiracles covered by pleural flaps.

Discussion. The previously held concept for the Tettigarctidae remains unchanged. All previously identified attributes for the Tettigarctidae remain applicable and are incorporated above (Evans, 1941; Moulds, 1990).

Bekker-Migdisova (1947) divided the Tettigarctidae by establishing the subfamily Cicadoprosbolinae, separating it from the Tettigarctinae by the following attributes: (*a*) fore wing elliptical with a broad costal area and clavus, (*b*) vein RP multibranched; (*c*) basal coalescence of veins M and Cu and (*d*) vein CuA not following nodal line (Wootton, 1971). This subfamily division is retained here following Boulard & Nel (1990) and Shcherbakov (in prep.).

Family Cicadidae Latreille, 1802

Cicadae *auct.*
Cicadides *auct.*
Cicadidae *auct.*
Cicadina *auct.*
Cicadinae *auct.*

For discussion on the authorship of family group names based on *Cicada* see notes under "Cicadidae/Cicadinae Latreille, 1802", p. 387.

Type genus. *Cicada* L. (type species *Cicada orni* L.).

Included subfamilies. Cicadinae Latreille, Cicadettinae Buckton **n.stat.**, Tettigadinae Distant.

Diagnosis. Thoracic ganglia fused. Pronotum smaller than mesonotum; paramedian and lateral fissures present; pronotal collar present. Mesonotum with a cruciform elevation. Fore wing vein RP arising from node; veins 2A and 3A fused; nodal line usually indistinct. Hind wing hamulus absent. Pretarsal empodia absent. Hind coxae not overhanging abdomen. Timbals present in males only. Male abdominal resonant chamber present. Tympana present in both sexes. Male sternite VIII shielding genitalia ventrally. Male genitalia with styles absent; basal lobe present; aedeagus never with a sclerotized subdorsal crest. Male reproductive system with testes located posteriorly, centred over abdominal sternite VI. Female genitalia either monotrysian or ditrysian. Female reproductive system with accessory glands of common oviduct present. Nymphs with antennal segments 1 (scape) and 2 (pedicel) together longer than segment 5 (3rd flagellomere); fore femur with no mid-lateral spine on outer face; fore tibiae subapical tooth absent or weakly developed and not opposing apical tooth; mid and hind tibiae with no stout spines along shank; hind tibiae with spines of spinal crown all similar.

Distinguishing characters. The following attributes are believed to differentiate the Cicadidae. Pronotum smaller than mesonotum; paramedian and lateral fissures present; pronotal collar present. Mesonotum with scutellum forming a cruciform elevation. Fore wing vein RP arising from node; veins 2A and 3A fused. Timbals present in males only or sometimes absent. Male abdominal resonant chamber present. Tympana present in both sexes. Male sternite VIII shielding genitalia ventrally. Male genitalia with basal lobes present. Male reproductive system with testes located posteriorly, centred over spiracles of sternite VI. Female reproductive system with accessory glands of common oviduct present. Nymphs with antennal segments 1 (scape) and 2 (pedicel) together longer than segment 5 (3rd flagellomere); fore femur with no mid-lateral spine on outer face; fore tibiae subapical tooth absent or weakly developed and not opposing apical tooth; mid and hind tibiae with no spines along shank; hind tibiae with spines of spinal crown all similar.

Discussion. The previously held concept of the Cicadidae remains unchanged. Previously identified attributes for the Cicadidae (Hayashi, 1984; Moulds, 1990) remain applicable.

Subfamily Cicadettinae Buckton, 1889, new status

Tibicinae *sensu* Buckton, 1889: 270.
Tibicininae *sensu* Distant, 1905b: 304.
Tibicinidae *sensu* Metcalf, 1939: 247.

The family-group name based upon *Tibicina* can no longer be applied to this subfamily as *Tibicina* now resides in the Tettigadinae. The oldest available family-group name associated with the genera now included is that based upon *Cicadetta*.

Type genus. *Cicadetta* Amyot (type species: *Cicada montana* Scopoli).

Included tribes. Carinetini Distant, Chlorocystini Distant, Cicadettini Buckton, Dazini Kato, Hemidictyini Distant, Huechysini Distant, Lamotialnini Boulard, Parnisini Distant, Prasiini Matsumura, Sinosenini Boulard, Taphurini Distant, Tettigomyiini Distant, Ydiellini Boulard **n.stat.**.

Diagnosis. Metanotum partly visible at dorsal midline. Fore wing veins CuP and 1A fused in part. Hind wing 1st cubital cell width at distal end much greater than 2nd cubital cell (twice or more); hind wing veins RP and M fused at base. Rim of male timbal cavity lacking a turned-back rim or timbal cover. Pygofer with distal shoulder undeveloped; pygofer upper lobe present. Claspers large, dominating the whole 10th abdominal segment. Uncus duck-bill shaped, small and flat. Aedeagus without ventrobasal pocket; aedeagus restrained by large claspers. Apical part of theca without leaf-like lateral lobes.

Distinguishing characters. Male genitalia with claspers large, dominating the whole 10th abdominal segment.

Discussion. The previously identified attribute for this subfamily, male abdominal timbal covers absent, remains applicable (Distant, 1905b; Kato, 1954; Boulard, 1976a; Hayashi, 1984; Moulds, 1990; Chou *et al.*, 1997). It is, however, insufficient alone to define the subfamily; timbal covers are also absent in the Tettigadinae.

Subfamily Cicadinae Latreille, 1802

Cicadinae *auct.*
Cicadidae *auct.*
Gaeaninae *auct.*
Tibiceninae *auct.*
Platypleurinae *auct.*

For discussion on nomenclature relating to synonymy see notes under "Cicadidae/Cicadinae Latreille, 1802" (p. 387), under "Platypleurinae Schmidt, 1918" (p. 388) and under "Tibiceninae Van Duzee, 1916" (p. 389).

Type genus. *Cicada* L. (type species *C. orni* L.).

Included tribes. Burbungini **n.tribe**, Cicadini Latreille, Cryptotympanini Handlirsch, Cyclochilini Distant, Distantadini Orian, Dundubiini Atkinson, Fidicinini Distant, Gaeanini Distant, Hamzini Distant, Hyantiini Distant, Jassopsaltriini **n.tribe**, Lahugadini Distant, Moganniini Distant, Oncotympanini Ishihara, Platypleurini Schmidt, Plautillini Distant **n.stat.**, Polyneurini Amyot & Serville, Psithyristriini Distant, Tacuini Distant, Talaingini Distant, Tamasini **n.tribe**, Thophini Distant, Zammarini Distant.

Diagnosis. Metanotum entirely concealed at dorsal midline. Fore wing veins CuP and 1A fused in part. Hind wing 1st cubital cell width at distal end about equal to 2nd cubital cell; hind wing veins RP and M fused at base. Abdominal timbal covers present. Pygofer with distal shoulder well developed, often the most distal part of pygofer and either broad and rounded or distally extended into a pointed lobe; pygofer upper lobe absent (except in some Cryptotympanini). Uncus of moderate length and retractable within pygofer. Claspers present or absent, if present then spined apically. Aedeagus without ventrobasal pocket; aedeagal restrained by tubular encapsulation below uncus. Apical part of theca without leaf-like lateral lobes.

Distinguishing characters. The following attributes define the Cicadinae: male abdominal timbal covers present, plus male pygofer with distal shoulder well developed, often the most distal part of pygofer, either broad and rounded or distally extended into a pointed lobe.

Discussion. The previously held concept of the Cicadinae remains substantially unchanged except that the subfamily Plautillinae is now included here at tribal rank. Previously identified attributes for this subfamily remain applicable (Hayashi, 1984; Moulds, 1990).

Subfamily Tettigadinae Distant, 1905

Tibicinae Buckton, 1889: 270 **n.syn.**
Tibicininae *sensu* Distant, 1905b: 304 (partim).
Tettigadinae Distant, 1905d: 479.
Tibicinidae *sensu* Metcalf, 1939: 247 (partim).
Platypediinae Kato, 1932 **n.syn.**

If one follows the principle of priority (*Code*, Article 23) then the name Tibicininae should take priority as it is the oldest available family-group name associated with the genera included in this new subfamily concept[1]. However, the name Tibicininae previously represented a major family group of quite different concept as discussed at length throughout much of this paper. To now change its meaning would not only cause confusion in this regard but more importantly perpetuate a multitude of digressions and confusion previously associated with it and which are well documented by Boulard (1988a, 1998, 2001). I therefore take this opportunity to abandon the use of the name Tibicininae and its family-group derivatives and adopt the next available family-group name, Tettigadinae, a name which not only lacks a history of confusion but also retains its meaning to a large extent in this new concept. Official use of Tettigadinae requires suppression of the name Tibicininae and its derivatives by the International Commission of Zoology Nomenclature (*Code*, Article 19); a case for suppression is in preparation.

Type genus. *Tettigades* Amyot & Serville (type species: *T. chilensis* Amyot & Serville).

Included tribes. Platypediini Kato, Tettigadini Distant, Tibicinini Distant.

Diagnosis. Metanotum entirely concealed at dorsal midline (except in *Platypedia* and *Tibicina*). Fore wing veins CuP and 1A unfused. Hind wing 1st cubital cell width at distal end about equal to 2nd cubital cell; veins RP and M unfused at their bases. Rim of abdominal timbal cavity with a turned-back rim. Pygofer with distal shoulder undeveloped; pygofer upper lobe absent. Uncus exceedingly long and non-retractable within pygofer. Claspers absent. Aedeagus with ventrobasal pocket present; aedeagal restrained by tubular encapsulation below uncus. Apical part of theca with a pair of leaf-like lateral lobes.

Distinguishing characters. Fore wing veins CuP and 1A not fused. Hind wing veins RP and M unfused at base. Uncus exceedingly long and non-retractable within pygofer. Aedeagus with ventrobasal pocket present. Aedeagus with apical part of theca bearing a pair of leaf-like lateral lobes and a non-retractable tubular vesica. The male opercula have a distinctive S-shape, their lateral margins deeply concave, distal margins not reaching distal margins of tympanal cavities, basally not extending beyond meracantha.

Discussion. This is an entirely new subfamily concept expanded to incorporate the former Tettigadinae, Platypediinae and the tribe Tibicinini. Previously identified attributes for the Tettigadinae in its former concept (Distant, 1905d; Jacobi, 1907b; Chen, 1943; Boulard, 1976a, 1986b; Hayashi, 1984; Duffels, 1993; Chou *et al*., 1997) are now applicable at tribal rank for the Tettigadini.

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[1] *Tibicina* is in fact a junior synonym of *Tibicen* (see discussion earlier in this paper under "Overview of family-group concepts, past and present", p. 393). However, the family group names based upon *Tibicina* retain their validity (see *Code*, Article 40.1) and the name Tibicininae remains available. Family group names based upon *Tibicina* predate those based upon *Tibicen*, and thus have priority.

A revised tribal classification for Australian Cicadidae

For tribal synonymies see Metcalf (1963) and Duffels & van der Laan (1985). Tribes are discussed below in alphabetical order by subfamilies. A summary of the revised classification of Australian cicadas is shown in Table 2.

Subfamily Cicadinae

Key to the tribes of Australian Cicadinae

Some characters used here for distinguishing Australian tribes may not be applicable to some non-Australian species belonging to these tribes.

1 Head with vertex very wide so that the supra-antennal plate clearly reaches less than half way to eye 2

—— Head with vertex of average width or narrow so that the supra-antennal plate reaches at least half way to eye 6

2 Epimeral lobe not reaching operculum .... Burbungini

—— Epimeral lobe reaching operculum 3

3 Fore leg femoral primary spine lying flat, prostrate .... Platypleurini

—— Fore leg femoral primary spine erect 4

4 Male 5

—— Female .... Cryptotympanini or Thophini

5 Timbal covers flat .... Cryptotympanini

—— Timbal covers inflated, sac-like .... Thophini

6 Pronotal collar with a single mid-lateral tooth; male opercula (of Australian species) very long, covering some ⅔ length of abdomen .... Dundubiini (subtribe Cosmopsaltriina)

—— Pronotal collar with lateral margin smooth; male opercula very long, covering some ⅔ length of abdomen 7

7 Head considerably less than width of pronotum; fore wing veins C and R + Sc widely separated .... Cyclochilini

—— Head about as wide as pronotum; fore wing veins C and R + Sc abutted for their length 8

8 Lateral ocelli widely separated, the distance between them about equal to the distance between each lateral ocellus and eye .... Jassopsaltriini

—— Lateral ocelli closely spaced, the distance between them considerably less than the distance between each lateral ocellus and eye .... Tamasini

Tribe Burbungini new tribe

Type genus. *Burbunga* Distant, 1905 (type species *Tibicen gilmorei* Distant).

Included genera. *Burbunga* Distant.

Diagnosis. Head with vertex laterally elongate so that eyes widely separated from supra-antennal plate. Postclypeus shape in transverse cross-section rounded; postclypeal ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margin weakly ampliate; lateral tooth absent. Fore wing pterostigma present; veins C and R+Sc close together; vein RA_1 aligned closely with subcosta (Sc) for its length. Hind wing with anal lobe broad and vein 3A curved at distal end, long, separated from wing margin. Fore leg femoral primary spine erect. Meracanthus gradually tapering to a point, triangular or nearly so. Male opercula completely encapsulating meracanthus and completely covering tympanal cavity. Male abdominal tergites with sides straight or convex in cross-section; tergites 2 and 3 similar in size to tergites 4–7; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals extend below wing bases. Timbal covers flat; reduced dorsally and not reaching metathorax; lower margin extending anteriorly from or very near auditory capsule. Pygofer upper lobe absent; basal lobe moderately to well developed; distal shoulder rounded, except in *Macrotristria hillieri* (not a true *Macrotristria*; its generic placement to be addressed in a forthcoming work, Moulds in prep.) where it is distally extended and pointed; dorsal beak present as a part of chitinized pygofer. Uncus digitate or basically tubular, long, dominant. Claspers absent. Aedeagus with basal portion of basal plate directed forwards away from thecal shaft; ventral rib completely fused with basal plate; theca recurved basally

Table 2. Summary of classification of Australian Cicadoidea.

old classification	**new classification**
family TETTIGARCTIDAE Distant	family TETTIGARCTIDAE Distant
subfamily TETTIGARCTINAE Distant	subfamily TETTIGARCTINAE Distant
tribe Tettigarctini Distant	tribe Tettigarctini Distant
Tettigarcta White	*Tettigarcta* White
family CICADIDAE Latreille	family CICADIDAE Latreille
subfamily CICADINAE Latreille	subfamily CICADINAE Latreille
tribe Platypleurini Schmidt	tribe Platypleurini Schmidt
subtribe Platypleurina Schmidt	*Oxypleura* Amyot & Serville
Oxypleura Amyot & Serville	
tribe Thophini Distant	tribe Thophini Distant
Thopha Amyot & Serville	*Thopha* Amyot & Serville
Arunta Distant	*Arunta* Distant
tribe Cryptotympanini Handlirsch	tribe Cryptotympanini Handlirsch
Anapsaltoda Ashton	*Anapsaltoda* Ashton
Neopsaltoda Distant	*Neopsaltoda* Distant
Psaltoda Stål	*Psaltoda* Stål
Macrotristria Stål	*Macrotristria* Stål
	Arenopsaltria Ashton
	Henicopsaltria Stål
tribe Cyclochilini Distant	tribe Cyclochilini Distant
Cyclochila Amyot & Serville	*Cyclochila* Amyot & Serville
Arenopsaltria Ashton	
Henicopsaltria Stål	
tribe Dundubiini Atkinson	tribe Dundubiini Atkinson
subtribe Cosmopsaltriina Kato	subtribe Cosmopsaltriina Kato
Diceropyga Stål	*Diceropyga* Stål
tribe Cicadini Oshanin	tribe Tamasini Moulds
Tamasa Distant	*Tamasa* Distant
Illyria Moulds	*Parnkalla* Distant
	tribe Burbungini Moulds
	Burbunga Distant
	tribe Jassopsaltriini Moulds
	Jassopsaltria Ashton
subfamily TIBICININAE Distant	subfamily CICADETTINAE Buckton
tribe Taphurini Distant	tribe Taphurini Distant
subtribe Taphurina Distant	subtribe Tryellina Moulds
Aleeta Moulds	*Aleeta* Moulds
Tryella Moulds	*Tryella* Moulds
Parnkalla Distant	*Chrysocicada* Boulard
Marteena Moulds	
Burbunga Distant	
tribe Parnisini Distant	
Chrysocicada Boulard	
Quintilia Stål	
Jassopsaltria Ashton	
Diemeniana Distant	
Gudanga Distant	
tribe Cicadettini Buckton	tribe Cicadettini Buckton
Kobonga Distant	*Kobonga* Distant
Pauropsalta Goding & Froggatt	*Pauropsalta* Goding & Froggatt
Notopsalta Dugdale	*Notopsalta* Dugdale
Kikihia Dugdale	*Kikihia* Dugdale
Birrima Distant	*Birrima* Distant
Urabunana Distant	*Urabunana* Distant
Cicadetta Amyot	*Cicadetta* Amyot
Froggattoides Distant	*Froggattoides* Distant
	Marteena Moulds
	Diemeniana Distant
	Gudanga Distant
tribe Prasiini Matsumura	tribe Prasiini Matsumura
Lembeja Distant	*Lembeja* Distant
tribe Chlorocystini Distant	tribe Chlorocystini Distant
Venustria Goding & Froggatt	*Venustria* Goding & Froggatt
Guineapsaltria Boer	*Guineapsaltria* Boer
Gymnotympana Stål	*Gymnotympana* Stål
Owra Ashton	*Owra* Ashton
Chlorocysta Westwood	*Chlorocysta* Westwood
Glaucopsaltria Goding & Froggatt	*Glaucopsaltria* Goding & Froggatt
Thaumastopsaltria Kirkaldy	*Thaumastopsaltria* Kirkaldy
Cystosoma Westwood	*Cystosoma* Westwood
Cystopsaltria Goding & Froggatt	*Cystopsaltria* Goding & Froggatt

through some 180°, overall spiral-shaped; pseudoparameres absent; subapical cerci absent. Male reproductive system with accessory glands long. Female reproductive system with length of accessory glands of common oviduct unknown.

Distinguishing characters. Head with vertex laterally elongate so that eyes widely separated from supra-antennal plate; theca spiral. Differs from the Platypleurini (which includes some species that are superficially similar to some Burbungini) by having the male timbal covers reduced dorsally.

Discussion. Support for the allocation of *Burbunga* to its own tribe is derived from its phylogenetic position in the cladistic analysis. It clearly differs from *Jassopsaltria* in head and aedeagal structure, and from *Cyclochila* in head shape, pronotal collar development, aedeagal structure and the shape of the male opercula.

Tribe Cryptotympanini Handlirsch, 1925

Cryptotympanaria Handlirsch, 1925: 1117.
Cryptotympanini Boulard, 1979b: 58–59.
Tibicenini Van Duzee, 1916: 55.
Lyristarini Gomez-Menor, 1957: 28.
Lyristini Boulard, 1972: 169.

Type genus. *Cryptotympana* Stål [type species: *Tettigonia atrata* F.; = *C. pustulata* (F.)].

Included genera. *Anapsaltoda* Ashton, *Antankaria* Distant, *Arenopsaltria* Ashton, *Cacama* Distant, *Chremistica* Stål, *Cornuplura* Davis, *Cryptotympana* Stål, *Diceroprocta* Stål, *Henicopsaltria* Stål, *Heteropsaltria* Jacobi, *Illyria* Moulds, *Lyristes* Horváth, *Macrotristria* Stål, *Neopsaltoda* Distant, *Nggeliana* Boulard, *Orialella* Metcalf, *Psaltoda* Stål, *Raiateana* Boulard, *Salvazana* Distant.

These genera are grouped into three subtribes: Cryptotympanina, Heteropsaltriina and Nggelianina based upon length of the fore wing cells and whether the timbal covers meet the opercula (Boulard, 1979b). Subtribes are not adopted here.

Diagnosis. Head with vertex laterally elongate so that eyes widely separated from supra-antennal plate. Postclypeus shape in transverse cross-section rounded; postclypeal ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margin strongly ampliate; lateral tooth absent. Fore wing pterostigma present; veins C and R+Sc close together; vein RA_1 aligned closely with subcosta (Sc) for its length. Hind wing with anal lobe broad and vein 3A usually curved at distal end, long, separated from wing margin. Fore leg femoral primary spine usually erect. Meracanthus gradually tapering to a point, triangular or nearly so. Male opercula completely encapsulating meracanthus and completely covering tympanal cavity. Male abdominal tergites with sides straight or convex in cross-section; tergites 2 and 3 larger than tergites 4–7; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals extend below wing bases. Timbal covers flat; fully rounded dorsally, extending to metathorax, tightly closing the timbal cavity or nearly so; lower margin extending anteriorly from or very near auditory capsule. Pygofer with upper lobe absent (except in *Henicopsaltria, Psaltoda, Anapsaltoda* and *Neopsaltoda*), thickened rather than flat; basal lobe moderately to well developed; distal shoulder rounded except in *Illyria* where it is distally extended and pointed; dorsal beak present as a part of chitinized pygofer (but absent in *Anapsaltoda, Henicopsaltria, Illyria, Neopsaltoda* and *Psaltoda*). Uncus digitate or basically tubular, large, dominant. Claspers absent. Aedeagus with basal portion of basal plate directed forwards away from thecal shaft; ventral rib completely fused with basal plate; theca recurved basally through some 180°; pseudoparameres absent; subapical cerci absent (except in *Illyria* and *Macrotristria*). Male reproductive system with length of accessory glands long. Female reproductive system with accessory glands of common oviduct short.

Distinguishing characters. Distinguished from the allied Platypleurini by having a broad head that is as wide or wider than the lateral margin of the pronotum (that of the Platypleurini is narrower, usually much narrower), and the head, thorax and abdomen are "normal" (unlike those of the Platypleurini which are compressed vertically, that is "flattened"). Distinguished from the allied Thophini by the male timbal covers that are flat (those of the Thophini are swollen and sack-like); females are not distinguishable.

Discussion. The Cryptotympanini as defined here is equivalent to Boulard's (1998) subtribe Cryptotympanaria. Boulard combined the Cryptotympanini and Platypleurini into the single tribe Platypleurini, with subtribes Cryptotympanaria and Platypleuraria. See further comments below under Platypleurini, p. 433.

Tribe Cyclochilini Distant, 1904

Cyclochilaria Distant, 1904a: 302.
Cyclochilini Kato, 1932: 144.

Type genus. *Cyclochila* Amyot & Serville (type species: *Tettigonia australasiae* Donovan).

Included genera. *Cyclochila* Amyot & Serville.

Diagnosis. Head with distance between supra-antennal plate and eye about equal to length of antennal plate. Postclypeus shape in transverse cross-section rounded; postclypeal ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margin strongly ampliate; lateral tooth absent; underside of lateral angles with stridulatory file (scraper on base of fore wing). Fore wing pterostigma present; veins C and R+Sc widely separated; vein R; A_1 aligned closely with subcosta (Sc) for its length. Hind wing with anal lobe broad and vein 3A curved at distal end, long, separated from wing margin. Fore leg femoral primary spine erect. Meracanthus rudimentary, short, worm-like. Male opercula completely encapsulating meracanthus and completely covering tympanal cavity. Male abdominal tergites with sides straight or convex in cross-section; tergites 2 and 3 similar in size to tergites 4–7; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals extend below wing bases. Timbal covers flat; reduced dorsally and not reaching metathorax; lower margin extending anteriorly from or very near auditory capsule. Pygofer upper lobe absent; basal lobe moderately to well developed; distal shoulder rounded; dorsal beak present as a part of chitinized pygofer (sometimes absent in *C. australasiae*). Uncus digitate or basically tubular, large, dominant. Claspers absent. Aedeagus with basal portion of basal plate directed forwards away from thecal shaft; ventral rib completely fused with basal plate; theca recurved basally through some 180°; pseudoparameres absent; subapical cerci absent. Male reproductive system with accessory glands long. Female reproductive system with accessory glands of common oviduct long.

Distinguishing characters. Pronotal collar with lateral margin strongly ampliate, evenly rounded and horizontal in lateral view; a stridulatory file on underside of lateral angles of pronotal collar and corresponding scraper on the base of the fore wing; male meracanthus is rudimentary, short and worm-like; fore wing veins C and R + Sc are widely separated; and the male reproductive system has extraordinary long vas deferentia and accessory glands. Differs from the Cryptotympanini, Platypleurini and Thophini also in having the timbal covers reduced dorsally and not reaching metathorax, and differs from most in the relatively narrow head that is much narrower than the ampliate pronotum and has the distance between the supra-antennal plate and eye about equal to the length of the antennal plate. Differs from the Burbungini and Jassopsaltriini also in having a broad lateral area to the pronotal collar, and in the male opercula which overlap and are well developed, and which reach well beyond the tympanal cavity.

Discussion. The separation of *Cyclochila* from the Thophini, Platypleurini, Cryptotympanini, Burbungini and Jassopsaltriini in the cladistic analysis justifies a tribal ranking based upon this genus only (see discussion "On the monophyly of the Cyclochilini", p. 423). Other genera previously assigned to the Cyclochilini belong to the Cryptotympanini.

Tribe Dundubiini Atkinson, 1886

Dundubia Atkinson, 1886: 157.
Dundubiaria Distant, 1905a: 58.
Dundubiini Schmidt, 1912: 65.
Dundubini Kato, 1956: 65.
Platylomiini China, 1964: 158.

Type genus. *Dundubia* (type species: *Tettigonia vaginata* F.).

Included genera. *Aceropyga* Duffels, *Aola* Distant, *Ayesha* Distant, *Ayuthia* Distant, *Basa* Distant, *Brachylobopyga* Duffels, *Calcagninus* Distant, *Cosmopsaltria* Stål, *Diceropyga* Stål, *Dilobopyga* Duffels, *Dokuma* Distant, *Dundubia* Amyot & Serville, *Euterpnosia* Matsumura, *Gudaba* Distant, *Haphsa* Distant, *Hyalessa* China, *Inthaxara* Distant, *Kamalata* Distant, *Khimbya* Distant, *Leptopsaltria* Stål, *Lethama* Distant, *Macrosemia* Kato, *Mata* Distant, *Maua* Distant, *Meimuna* Distant, *Moana* J.G. Myers, *Nabalua* Moulton, *Orientopsaltria* Kato, *Platylomia* Stål, *Purana* Distant, *Puranoides* Moulton, *Rhadinopyga* Duffels, *Rustia* Stål, *Semia* Matsumura, *Sinapsaltria* Kato, *Sinosemia* Matsumura, *Taiwanosemia* Matsumura, *Tanna* Distant, *Terpnosia* Distant, *Tosena* Amyot & Serville, *Trengganua* Moulton.

These genera are grouped into five subtribes: Terpnosiina Kato, Leptopsaltriina Moulton, Dundubiina Matsumura, Cosmopsaltriina Kato and Tosenina Amyot & Serville. Only the subtribe Cosmopsaltriina is relevant to the Australian fauna, see below.

Diagnosis. Head with distance between supra-antennal plate and eye about equal to length of antennal plate. Postclypeus shape in transverse cross-section rounded; postclypeal ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margin weakly ampliate; lateral tooth present. Fore wing pterostigma present; veins C and R+Sc close together; vein RA_1 aligned closely with subcosta (Sc) for its length. Hind wing with anal lobe narrow and vein 3A straight, short, adjacent to wing margin. Fore leg femoral primary spine erect. Meracanthus gradually tapering to a point, triangular or nearly so. Male opercula very long, reaching far beyond tympanal cavity to cover some two thirds length of abdomen, clearly separated. Male abdominal tergites with sides straight or convex in cross-section; tergites 2 and 3 similar in size to tergites 4–7; epipleurites reflexed to ventral surface, epipleurite 4, and sometimes also others, strongly kinked inwards in a V-shape. Timbals extend below wing bases. Timbal covers flat; fully rounded dorsally, extending to metathorax, tightly closing the timbal cavity or nearly so; lower margin extending vertically from auditory capsule before turning anteriorly. Pygofer upper lobe absent; basal lobe moderately to well developed; distal shoulder distally extended into pointed, and often apically up-turned, lobe (except in subtribe Dundubiina); dorsal beak present, either as a flap on "hinge" tissue or, in Cosmopsaltriina a part of chitinized pygofer. Uncus digitate or basically tubular, long, dominant and often deeply divided into lateral lobes; claspers absent in subtribe Dundubiina, present in subtribe Cosmopsaltriina. Aedeagus with basal portion of basal plate directed forwards away from thecal shaft; ventral rib completely fused with basal plate; theca recurved basally through some 180° in subtribe Dundubiina, straight or curved in a gentle arc in subtribe Cosmopsaltriina; pseudoparameres absent; subapical cerci absent. Male reproductive system with accessory glands long. Female reproductive system with length of accessory glands of common oviduct unknown.

Distinguishing characters. Pronotal collar with lateral tooth. Hind wing with anal lobe narrow and vein 3A straight, short, adjacent to wing margin. Male opercula very long, reaching far beyond tympanal cavity to cover some two thirds length of abdomen, clearly separated; tergites 2 and 3 much enlarged, 2+3 usually accounting for approximately half abdominal length. Timbal covers fully rounded dorsally, extending to metathorax, tightly closing the timbal cavity or nearly so. Pygofer dorsal beak present as a flap on "hinge" membrane.

Discussion. Lee & Hayashi (2003) combine the Dundubiini and Cicadini. They retain the name Dundubiini, placing Cicadini in synonymy although strictly speaking Cicadini has priority (see discussion under Dundubiini p. 391 above). I am tentatively retaining the Dundubiini in anticipation of an overview of these two tribes.

Primary attributes of earlier authors that are retained here include the presence of a lateral tooth on the pronotal collar and the characteristic elongation of the male opercula. Of the subtribes currently recognized only the Cosmopsaltriina is represented in Australia.

Subtribe Cosmopsaltriina Kato, 1932

Cosmopsaltriaria Kato, 1932: 145.
Cosmopsaltriina Duffels & Turner, 2002: 235.

Type genus. *Cosmopsaltria* Stål (type species: *Cicada doryca* Boisduval).

Included genera. *Aceropyga* Duffels, *Brachylobopyga* Duffels, *Cosmopsaltria* Stål, *Diceropyga* Stål, *Dilobopyga* Duffels, *Meimuna* Distant, *Moana* J.G. Myers, *Rhadinopyga* Duffels (*sensu* Duffels, 1983, 1993; Beuk, 2002).

Diagnosis. Distal shoulder distally extended into pointed, and often apically up-turned lateral lobe. Accessory spines (claspers) present. Theca straight or curved in a gentle arc and with fleshy apical appendages.

Distinguishing characters. As for diagnosis above but the extended and apically up-turned lateral lobes of the male pygofer distal shoulder are similar in some Burbungini and rudimentary in Thophini. A straight or curved theca is also widespread within the Cicadidae but the fleshy apical appendages are characteristic for the Cosmopsaltriina.

Discussion. The concept of the Cosmopsaltriina has been reviewed by Duffels (1983, 1986, 1993, 1997) and Beuk (2002). Readers are directed to these studies for detailed species accounts and their phylogenetic relationships.

Tribe Jassopsaltriini new tribe

Type genus. *Jassopsaltria* Ashton (type species: *J. rufifacies* Ashton).

Included genera. *Jassopsaltria* Ashton.

Diagnosis. Head with distance between supra-antennal plate and eye about equal to length of antennal plate; antennal plate produced into a pointed lobe; eyes very small but head is broad so that the distance between the lateral ocelli is about equal to the breadth of each eye. Postclypeus shape in transverse cross-section rounded; postclypeal ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margin weakly ampliate; lateral tooth absent. Fore wing pterostigma present; veins C and R+Sc close together; vein RA_1 aligned closely with subcosta (Sc) for its length. Hind wing with anal lobe broad and vein 3A curved at distal end, long, separated from wing margin. Fore leg femoral primary spine erect. Meracanthus gradually tapering to a point, triangular or nearly so. Male opercula not completely encapsulating meracanthus, and entirely covering tympanal cavity. Male abdominal tergites with sides straight or convex in cross-section; tergites 2 and 3 a little larger than to tergites 4–7; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals extend below wing bases. Timbal covers flat; reduced dorsally and not reaching metathorax; lower margin extending anteriorly from or very near auditory capsule. Pygofer upper lobe thickened rather than flat; basal lobe moderately to well developed; distal shoulder rounded; dorsal beak absent. Uncus digitate or basically tubular, large, dominant. Claspers absent. Aedeagal basal plate with basal portion directed forwards away from thecal shaft; ventral rib completely fused with basal plate; theca recurved basally through some 180°, J-shaped; pseudoparameres absent; subapical cerci absent. Male reproductive system with length of accessory glands unknown. Female reproductive system with length of accessory glands of common oviduct unknown.

Distinguishing characters. Eyes are very small but the head is broad so that the distance between the lateral ocelli is about equal to the breadth of each eye; pygofer dorsal beak absent.

Discussion. The differentiation of *Jassopsaltria* in the cladistic analysis supports a tribal ranking based upon this genus only. It clearly differs from its putative sister group, the Burbungini, in head shape, by lacking a dorsal beak on the male pygofer and the aedeagus is J-shaped rather than spiralled.

Tribe Platypleurini Schmidt, 1918

Platypleurini Schmidt, 1918: 378.
Platypleurinae Handlirsch, 1925: 1117.
Cryptotympanini Handlirsch, 1925 (*partim*).–Boulard, 1998: 117.

Type genus. *Platypleura* Amyot & Serville (type species *Cicada stridula* L.).

Included genera. *Afzeliada* Boulard, *Attenuella* Boulard, *Brevisiana* Boulard, *Esada* Boulard, *Hainanosemia* Kato, *Ioba* Distant, *Kalabita* Moulton, *Karscheliana* Boulard, *Koma* Distant, *Kongota* Distant, *Muansa* Distant, *Munza* Distant, *Oxypleura* Amyot & Serville, *Platypleura* Amyot & Serville, *Pycna* Amyot & Serville, *Sadaka* Distant, *Severiana* Boulard, *Soudaniella* Boulard, *Strumosella* Boulard, *Suisha* Kato, *Ugada* Distant, *Umjaba* Distant, *Yanga* Distant.

Diagnosis. Head with vertex laterally elongate so that eyes widely separated from supra-antennal plate. Postclypeus shape in transverse cross-section rounded; postclypeal ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margin strongly ampliate; lateral tooth absent. Fore wing pterostigma present; veins C and R+Sc close together; vein RA_1 aligned closely with subcosta (Sc) for its length. Hind wing with anal lobe broad and vein 3A usually curved at distal end, long, separated from wing margin. Fore leg femoral primary spine usually laying flat, prostrate, but sometimes erect. Meracanthus gradually tapering to a point, triangular or nearly so. Male opercula completely encapsulating meracanthus and completely covering tympanal cavity. Male abdominal tergites with sides straight or convex in cross-section; tergites 2 and 3 a little larger than tergites 4–7; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals extend below wing bases. Timbal covers flat; fully rounded dorsally, extending to metathorax, tightly closing the timbal cavity or nearly so; lower margin extending anteriorly from or very near auditory capsule. Pygofer with upper lobe absent; basal lobe moderately to well developed; distal shoulder rounded; dorsal beak a part of chitinized pygofer. Uncus digitate or basically tubular, large, dominant. Claspers absent. Aedeagus with basal portion of basal plate directed forwards away from thecal shaft; ventral rib completely fused with basal plate; theca straight or curved in a gentle arc; pseudoparameres absent; subapical cerci absent. Male reproductive system with length of accessory glands unknown. Female reproductive system with length of accessory glands of common oviduct unknown.

Distinguishing characters. Head, thorax and abdomen vertically compressed; pronotal collar with lateral margin strongly ampliate so that head is always narrower than the pronotum; fore leg femoral primary spine nearly always prostrate; theca straight or curved in an arc. In some genera the strongly ampliate lateral margin to the pronotal collar is characteristically sharply angular around mid point.

Discussion. Boulard (1998) has suggested that the Cryptotympanini be included in the Platypleurini. The cladistic analysis implies that the Thophini would also have to be included in such an arrangement. Although there is a lack of strong synapomorphies for distinguishing the Platypleurini, Cryptotympanini and Thophini I believe they are sufficiently different to warrant individual tribal status; males especially are easily recognized.

Former subtribal groupings within the Platypleurini [Platypleurina, (= Platypleuraria *auct.*) and Hainanosemiina (= Hainanosemiaria *auct.*) are here abandoned as they lack sufficient differentiation.

Tribe Tamasini new tribe

Type genus. *Tamasa* Distant (type species *Cicada tristigma* Germar).

Included genera. *Tamasa* Distant and *Parnkalla* Distant.

Diagnosis. Head with distance between supra-antennal plate and eye about equal to length of antennal plate. Postclypeus shape in transverse cross-section rounded; postclypeal ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margin weakly ampliate or confluent with adjoining pronotal sclerites; lateral tooth absent. Fore wing pterostigma present; veins C and R+Sc close together; vein RA_1 aligned closely with subcosta (Sc) for its length. Hind wing with anal lobe broad and vein 3A curved at distal end, long, separated from wing margin. Fore leg femoral primary spine erect. Meracanthus gradually tapering to a point, triangular or nearly so. Male opercula not completely encapsulating meracanthus, covering tympanal cavity but not meeting. Male abdominal tergites with sides straight or convex in cross-section; tergites 2 and 3 similar in size to tergites 4–7; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals extend below wing bases; timbal covers flat, small, reduced dorsally and ventrally and not reaching metathorax. Pygofer with upper lobe absent; pygofer basal lobe moderately to well developed; dorsal beak a part of chitinized pygofer. Uncus digitate or basically tubular, large, dominant. Claspers absent. Aedeagus with ventral rib completely fused with basal plate; theca straight or curved in a gentle arc; pseudoparameres absent; subapical cerci absent. Male reproductive system with accessory glands short. Female reproductive system with accessory glands of common oviduct long.

Distinguishing characters. Aedeagus with basal portion of basal plate directed upwards and nearly parallel with thecal shaft; the basal plate is also deeply divided and Y-shaped in dorsal view. The broad head (distance between supra-antennal plate and eye about equal to length of supra-antennal plate) in conjunction with a very elongate basal cell on the fore wing distinguish members of this tribe from all other Australian tribes except the Dundubiini. The Dundubiini differ by having a mid lateral tooth on the pronotal collar. The male timbal covers of the Tamasini are very short and their leading margin is curled upwards for part or all of their length.

Discussion. The clear separation of the monophyletic group comprising *Tamasa* and *Parnkalla* in the cladistic analysis provides strong support for the tribal ranking for these genera. The Tamasini do not appear to be closely allied to any other Australian tribe.

Tribe Thophini Distant, 1904

Thopharia Distant, 1904a: 301.
Thophini Kato, 1932: 144.

Type genus. *Thopha* Amyot & Serville (type species *Tettigonia saccata* F.).

Included genera. *Arunta* Distant, *Thopha* Amyot & Serville.

Diagnosis. Head with vertex laterally elongate so that eyes widely separated from supra-antennal plate. Postclypeus shape in transverse cross-section rounded; postclypeal ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margin strongly ampliate (except in *Arunta*); lateral tooth absent. Fore wing pterostigma present; veins C and R+Sc close together; vein RA_1 aligned closely with subcosta (Sc) for its length. Hind wing with anal lobe broad and vein 3A usually curved at distal end, long, separated from wing margin. Fore leg femoral primary spine erect. Meracanthus gradually tapering to a point, triangular or nearly so. Male opercula completely encapsulating meracanthus and completely covering tympanal cavity. Male abdominal tergites with sides straight or convex in cross-section; tergites 2 and 3 a little larger than tergites 4–7; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals extend below wing bases. Timbal covers swollen and sac-like; fully rounded dorsally, extending to metathorax, tightly closing the timbal cavity or nearly so; lower margin extending anteriorly from or very near auditory capsule. Pygofer with upper lobe absent; basal lobe moderately to well developed; distal shoulder rounded; dorsal beak a part of chitinized pygofer. Uncus digitate or basically tubular, large, dominant. Claspers absent. Aedeagus with basal portion of basal plate directed forwards away from thecal shaft; ventral rib completely fused with basal plate; theca straight or curved in a gentle arc; pseudoparameres absent; subapical cerci absent. Male reproductive system with length of accessory glands long. Female reproductive system with length of accessory glands of common oviduct long.

Distinguishing characters. Males are readily distinguished by their greatly swollen and sac-like timbal covers. Females differ from those of the allied Platypleurini in having a head that is wider than the pronotum; the head of Platypleurini is narrower, usually much narrower. Females are similar to some Cryptotympanini.

Discussion. The Cuban genus *Uhleroides* has recently been transferred to the South American tribe Zammarini (Moulds, 2001). Although males of some species show some sac-like development of the timbal covers, the covers are much reduced dorsally. Further, the male aedeagus of *Uhleroides* is markedly different and the postclypeal ridges have transverse grooves. These are all features of the Zammarini.

Subfamily Cicadettinae n.stat.

Key to the tribes of Australian Cicadettinae (= Tibicininae *auct.*)

Some characters used here for distinguishing Australian tribes may not be applicable to some non-Australian species belonging to these tribes.

1	Fore wing with 9 or more apical cells	2
——	Fore wing with 8 apical cells	3
2	Head narrower than maximum width of pronotum	Chlorocystini
——	Head wider than maximum width of pronotum	Taphurini (subtribe Tryellina)
3	Fore wing costa broadest near node	Chlorocystini
——	Fore wing costa not broadest near node, tending to be parallel-sided	4
4	Hind wing veins CuP and 1A fused in part	Prasiini
——	Hind wing veins CuP and 1A unfused	5
5	Fore wing veins M and CuA meeting the basal cells with their stems confluent	Cicadettini
——	Fore wing veins M and CuA meeting the basal cell clearly separated	6
6	Male	7
——	Female	Cicadettini or Taphurini (subtribe Tryellina)
7	Opercula within confines of tympanal cavity	Cicadettini
——	Opercula extending distally beyond tympanal cavity	Taphurini (subtribe Tryellina)

Tribe Chlorocystini Distant, 1905

Chlorocystaria Distant, 1905f: 212.
Chlorocystini Handlirsch, 1925: 1116.
Gymnotympanini Boulard, 1979a.–Boer, 1995: 204.
Hemidictyini Distant, 1905g (*partim*).–Boer, 1995b: 204.

Type genus. *Chlorocysta* Westwood (type species: *Cystosoma vitripennis* Westwood).

Included genera. *Aedeastria* Boer, *Baeturia* Stål, *Chlorocysta* Westwood, *Cystopsaltria* Goding & Froggatt, *Cystosoma* Westwood, *Glaucopsaltria* Goding & Froggatt, *Guineapsaltria* Boer, *Gymnotympana* Stål, *Mirabilopsaltria* Boer, *Owra* Ashton, *Papuapsaltria* Boer, *Scottotympana* Boer, *Thaumastopsaltria* Stål, and *Venustria* Goding & Froggatt.

Diagnosis. Head with supra-antennal plate meeting or nearly meeting eye. Postclypeus shape in transverse cross-section angular; postclypeal ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margin confluent with adjoining pronotal sclerites; lateral tooth absent. Fore wing pterostigma absent; veins C and R+Sc close together; vein RA_1 diverging from subcosta (Sc) in subapical region (except in *Thaumastopsaltria, Cystosoma* and *Cystopsaltria*). Hind wing with anal lobe broad (except in *Gymnotympana*) and vein 3A usually curved at distal end, long, separated from wing margin. Fore leg femoral primary spine erect (except in *Thaumastopsaltria, Cystosoma* and *Cystopsaltria*). Meracanthus gradually tapering to a point, triangular or nearly so. Male opercula not completely encapsulating meracanthus and partly covering tympanal cavity. Male abdominal tergites with sides partly concave in cross-section; tergites 2 and 3 similar in size to tergites 4–7; epipleurites rounded to ventral surface, without an inward V-shaped kink. Timbals extend below wing bases. Timbal covers absent. Pygofer with upper lobe present (except in *Venustria*), thickened rather than flat; basal lobe ill-defined, substantially confluent with pygofer margin; dorsal beak present as a part of chitinized pygofer. Uncus absent. Claspers large, dominating the whole 10th abdominal segment. Aedeagus with basal portion of basal plate directed forwards away from thecal shaft; ventral rib completely fused with basal plate; theca "S" shaped; pseudoparameres absent; subapical cerci absent. Male reproductive system with accessory glands either short or long. Female reproductive system with accessory glands of common oviduct either short or long.

Distinguishing characters. The tribe is primarily characterized by the "S" shaped theca (Boer, 1995b). Other features include the inflated male abdomen with epipleurites rounded to the ventral surface and fore wing vein RA_1 diverging from subcosta (Sc) in subapical region (except in *Thaumastopsaltria, Cystosoma* and *Cystopsaltria*).

Discussion. The concept of the Chlorocystini remains unchanged from that of Boer (1995b). His extensive review of the tribe should be consulted for ingroup relationships and species reviews.

Tribe Cicadettini Buckton, 1889

Cicadinae Buckton, 1889: 270.
Cicadetta Buckton, 1890: xxxiv.
Melampsaltaria Distant, 1905g: 269.
Cicadettaria Oshanin, 1908: 396.
Melampsaltini Van Duzee, 1916: 57.
Cicadettini Boulard, 1972: 70.

Type genus. *Cicadetta* Amyot (type species: *Cicada montana* Scopoli).

Included genera. *Amphipsalta* Fleming, *Auta* Distant, *Birrima* Distant, *Buyisa* Distant, *Cicadetta* Amyot, *Cicadivetta* Boulard, *Curvicicada* Chou & Lu, *Diemeniana* Distant, *Euryphara* Horváth, *Fijipsalta* Duffels, *Froggattoides* Distant, *Gudanga* Distant, *Hilaphura* Webb, *Kikihia* Dugdale, *Kobonga* Distant, *Leptopsalta* Kato, *Linguacicada* Chou & Lu, *Maoricicada* Dugdale, *Marteena* Moulds, *Melampsalta* Kolenati, *Mouia* Distant, *Myersalna* Boulard, *Nigripsaltria* Boer, *Notopsalta* Dugdale, *Pagiphora* Horváth, *Pauropsalta* Goding & Froggatt, *Pinheya* Dlabola, *Poviliana* Boulard, *Rhodopsalta* Dugdale, *Saticula* Stål, *Scolopita* Chou and Lei, *Stellenboschia* Distant, *Takapsalta* Matsumura, *Tettigetta* Kolenati, *Tibeta* Lei & Chou, *Toxopeusella* Kirkaldy, *Urabunana* Distant, *Xossarella* Boulard; a new genus represented by *Abricta borealis*; a new genus represented by *Quintilia infans*.

Note that *Diemeniana, Gudanga* and *Quintilia infans* were previously attributed to the Parnisini and *Marteena* and *Abricta borealis* to the Taphurini.

Diagnosis. Head with supra-antennal plate meeting or nearly meeting eye. Postclypeus shape in transverse cross-section rounded; postclypeal ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margin weakly ampliate or confluent with adjoining pronotal sclerites; lateral tooth absent (except in *Diemeniana, Kobonga, Marteena, Pauropsalta* and in the new genus represented by *Abricta borealis*). Fore wing pterostigma present; veins C and R+Sc close together; vein RA_1 aligned closely with subcosta (Sc) for its length. Hind wing with anal lobe broad (except in *Froggattoides*) and vein 3A usually curved at distal end, long, separated from wing margin. Fore leg femoral primary spine erect. Meracanthus gradually tapering to a point, triangular or nearly so. Male opercula not completely encapsulating meracanthus and partly or entirely covering tympanal cavity. Male abdominal tergites with sides straight or convex in cross-section; tergites 2 and 3 similar in size to tergites 4–7; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals not extended below wing bases; timbal covers absent. Pygofer with upper lobe present (except in *Froggattoides* and in the new genus represented by *Cicadetta forresti*), flat; basal lobe moderately to well developed; dorsal beak present as a part of chitinized pygofer. Uncus duck-bill shaped, very broad and flat. Claspers large, dominating the whole 10th abdominal segment. Aedeagus with basal portion of plate basal directed forwards away from thecal shaft; ventral rib completely fused with basal plate; theca straight or curved in a gentle arc; pseudoparameres present; subapical cerci absent. Male reproductive system with accessory glands short. Female reproductive system with accessory glands of common oviduct usually long, sometimes short.

Distinguishing characters. Timbals not extended below wing bases; pygofer upper lobe flat (missing in *Froggattoides*); pseudoparameres present.

Discussion. The traditional concept of the Cicadettini, based on the basal coalescence of fore wing veins M and CuA, is here very much altered. While the coalescence of these veins was a convenient means of recognizing most members of this tribe, the attribute unfortunately sometimes is contradictory. In some genera such as *Pauropsalta* some species show coalescence but in others these veins are entirely separated, and in some species such as *Kobonga umbrimargo* some individuals clearly lack fusion. See discussion above under the heading "Some notable characters trends", p. 412, for further comments on this matter.

Tribe Prasiini Matsumura, 1917

Prasinaria Matsumura, 1917: 209.
Prasiini Kato, 1932: 188.
Prasiinae Jacobi, 1941: 317.
Prasini Kato, 1956: 65.

Type genus. *Prasia* Stål (type species *P. faticina* Stål).

Included genera. *Arfaka* Distant, *Iruana* Distant, *Jacatra* Distant, *Lacetas* Karsch, *Lembeja* Distant, *Prasia* Stål and *Sapantanga* Distant.

Diagnosis. Head with supra-antennal plate meeting eye. Postclypeus shape in transverse cross-section angular; postclypeal ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margin confluent with adjoining pronotal sclerites; lateral tooth absent. Fore wing pterostigma present; veins C and R+Sc close together; vein RA_1 aligned closely with subcosta (Sc) for its length. Hind wing with anal lobe either broad or narrow and vein 3A either separated or adjacent to wing margin. Fore leg femoral primary spine erect. Meracanthus gradually tapering to a point, triangular or nearly so. Male opercula not completely encapsulating meracanthus and partly covering tympanal cavity. Male abdominal tergites with sides straight or convex in cross-section; tergites 2 and 3 similar in size to tergites 4–7; epipleurites reflexed to ventral surface, without an inward V-shaped kink. Timbals extend below wing bases; timbal covers absent. Pygofer with upper lobe present, thickened rather than flat; pygofer basal lobe development ill-defined, substantially confluent with pygofer margin; dorsal beak a part of chitinized pygofer. Uncus absent. Claspers large, dominating the whole 10th abdominal segment. Aedeagus with basal portion of basal plate directed forwards away from thecal shaft; ventral rib completely fused with basal plate. Theca straight or curved in a gentle arc; pseudoparameres absent; subapical cerci absent. Male and female reproductive systems unknown.

Distinguishing characters. The four apomorphies identified by Boer (1995b, 1997) as distinguishing the Prasiini are not in dispute and are here accepted as defining the Prasiini *sensu* Jong (1982, 1985, 1986, 1987) and Boer (1995b, 1997), *viz.* a very narrow vertex with ocelli close together; a large obconical and triangularly protruding postclypeus; a very narrow hyaline border along hind margin of hind wing; well-developed and posteriorly projecting protuberances on upper pygofer lobes of male.

Discussion. The inclusion of the African genera here is tentative and awaits a broad assessment of the tribe and allied genera.

Tribe Taphurini Distant, 1905

Taphuraria Distant, 1905e: 25.
Lemuriaria Moulton, 1923: 78.
Eaphurarini [sic] Lallemand, 1925: 2.
Taphurini Kato, 1932: 171.

Type genus. *Taphura* Distant (type species *T. misella* Stål).

Included genera. *Abricta* Stål, *Abroma* Stål, *Aleeta* Moulds, *Chrysocicada* Boulard, *Dorachosa* Distant, *Dulderana* Distant, *Elachysoma* Torres, *Hea* Distant, *Hylora* Boulard, *Imbabura* Distant, *Kanakia* Distant, *Lemuriana* Distant, *Ligymolpa* Karsch, *Magicicada* Davis, *Malagasia* Distant, *Malgachialna* Boulard, *Monomatapa* Distant, *Musimoia* China, *Nelcyndana* Distant, *Neomuda* Distant, *Nosola* Stål, *Oudeboschia* Distant, *Panka* Distant, *Prosotettix* Jacobi, *Psallodia* Uhler, *Selymbria* Stål, *Taphura* Stål, *Trismarcha* Karsch, *Tryella* Moulds, *Ueana* Distant, *Viettealna* Boulard; a new genus represented by *Abricta occidentalis*.

Note that *Magicicada* was previously attributed to the Tibicinini and *Chrysocicada* to the Parnisini.

Diagnosis. Head with supra-antennal plate meeting or nearly meeting eye (except in *Aleeta* and *Tryella*). Postclypeus shape in transverse cross-section rounded; postclypeal ridges lacking transverse grooves towards distal ends. Pronotal collar with lateral margin weakly ampliate or confluent with adjoining pronotal sclerites; lateral tooth absent (except in *Magicicada*). Fore wing pterostigma present; veins C and R+Sc close together; vein RA_1 aligned closely with subcosta (Sc) for its length. Hind wing with anal lobe broad and vein 3A usually curved at distal end, long, separated from wing margin. Fore leg femoral primary spine erect. Meracanthus gradually tapering to a point, triangular or nearly so. Male opercula not completely encapsulating meracanthus, partly or entirely covering tympanal cavity but never extending beyond midlength of abdomen. Male abdominal tergites with sides straight or convex in cross-section; tergites 2 and 3 similar in size to tergites 4–7; epipleurites reflexed to ventral surface (except in *Magicicada*), without an inward V-shaped kink. Timbals extend below wing bases. Pygofer with upper lobe either present or absent, flat; pygofer basal lobe moderately to well developed; dorsal beak a part of chitinized pygofer. Uncus absent. Claspers large, dominating the whole 10th abdominal segment, often widely separated. Aedeagus with basal portion basal plate directed forwards away from thecal shaft; ventral rib rod-like, suspended with attachment only at ends; theca either recurved basally through 140° or lacking a pronounced basal recurve; pseudoparameres absent; subapical cerci absent. Male reproductive system with accessory glands long in *Aleeta*, otherwise unknown. Female reproductive system with accessory glands of common oviduct long in *Aleeta*, otherwise unknown.

Distinguishing characters. Males differ from other members of the subfamily Cicadettinae by having the aedeagal basal plate with the ventral rib rod-like, suspended with attachments only at ends. The claspers are widely separated except in *Abricta occidentalis* that represents a new genus. Males can be distinguished from those of the Cicadettini by having the timbals not extending below the level of the wing bases, and the timbal ribs are long and closely spaced and at least 5 in number. Females differ from the Chlorocystini and Prasiini by having the head broader than the maximum width of the pronotum. Females cannot be distinguished from those of the Cicadettini in which the fore wing veins M and CuA meet the basal cell separated.

Discussion. Attributes previously defining the Taphurini still apply but are insufficient for unique characterization. Differences between the type genus from South America (and its allies) and other Taphurini are considered sufficiently distinct to warrant division of the tribe into two subtribes.

The nominotypical subtribe Taphurina Distant has no Australian representative. Included genera are *Dorachosa* Distant, *Dulderana* Distant, *Elachysoma* Torres, *Imbabura* Distant, *Nosola* Stål, *Prosotettix* Jacobi, *Selymbria* Stål and *Taphura* Stål, although some genera allocated here may be incorrectly placed as it was not possible to examine examples of all genera. The diagnostic features of the subtribe Taphurina are as follows: Male aedeagus lacks a strong basal recurve of the theca and the upper pygofer lobe is absent; the male opercula curve towards abdominal midline but are very small, narrow, and remain widely separated and far from the distal margins of the tympanal cavities.

Subtribe Tryellina new subtribe

Type genus. *Tryella* Moulds (type species *T. ochra* Moulds).

Included genera. *Abricta* Stål, *Abroma* Stål, *Aleeta* Moulds, *Chrysocicada* Boulard, *Hylora* Boulard, *Kanakia* Distant, *Lemuriana* Distant, *Ligymolpa* Karsch, *Magicicada* Davis, *Malagasia* Distant, *Malgachialna* Boulard, *Monomatapa* Distant, *Musimoia* China, *Nelcyndana* Distant, *Neomuda* Distant, *Oudeboschia* Distant, *Panka* Distant, *Trismarcha* Karsch, *Tryella* Moulds, *Ueana* Distant, *Viettealna* Boulard; a new genus represented by *Abricta occidentalis*.

Some genera allocated here may be incorrectly placed as it was not possible to examine examples of all genera.

Diagnosis. Male theca recurved basally through some 140° and the male upper pygofer lobe present. The male opercula tend linear and reach beyond the tympanal cavities.

Distinguishing characters. See diagnosis above.

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